SYSTEMATICS AND EVOLUTION OF THE GENUS *TRIODOPSIS* (MOLLUSCA: PULMONATA: POLYGYRIDAE)

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CONTENTS

INTRODUCTION

The purpose of this work was to study the evolutionary biology of the genus *Triodopsis*. This is one of the most common genera of land snails in eastern North America, yet no comprehensive, modern work has been done on its systematics or evolution. Our knowledge concerning the group still comes mainly from the work of Pilsbry (1940) and Hubricht (1949; 1950a, b; 1952a, b; 1953; 1954; 1958). Perhaps it is permissible to say that, although valuable, these works are not based on modern conceptions of species, speciation, etc., but solely upon morphology. Thus it seemed that a restudy of the group was needed.

The results of this study are consistent with the tenets of the evolutionary theory. Of interest are the high frequency of hybridization and the rarity of clines. The new classification is both simpler and more consistent than the previous one.

Material was studied from various sources. Most important were the Museum of Comparative Zoology (MCZ) and the Academy of Natural Sciences of Philadelphia (ANSP). I also received some material from the Carnegie Museum of Pittsburgh (CM), the United States National Museum (USNM), and Mr. Leslie Hubricht, of Meridian, Mississippi. Finally, I obtained some material from my own field trips (JV). Four extensive collecting trips were made, each lasting eight to fifteen days, and several shorter ones. These covered an area extending from the Atlantic Coast to Illinois and Texas.

The following working methods were used. First, all the available samples of each species were surveyed. Then measurements of from three to eight characters were taken on representative samples from the various parts of the range, and the re-

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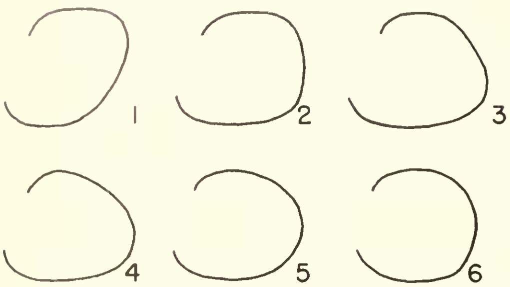

Figure 1. Aperture shape in *Triadopsis*. 1, Auriculate; 2, square; 3, trapezoid; 4, triangular; 5, oval; 6, circular.

sults obtained evaluated statistically. The distribution and ecology were then studied by plotting the records on large scale maps showing hydrography, vegetation, and elevation. Information on the distribution and ecology were also taken from the literature. In the last step, the data obtained from these various sources were synthesized.

Many of the terms used in this paper occur commonly in the literature, but some do not. Definitions of the necessary terms follow.

Aperture: the margin of the shell that surrounds the opening of the shell; also the surrounded area. The shape of the aperture may be auricular, square, trapezoid, triangular, oval, round, or intermediate between any of these (Fig. 1). These geometrical forms are actually never "complete," in the sense that the upper left corner is always truncated by the penultimate whorl. The term aperture is interchangeable with lip or peristome.

Aperture grade: the degree of development of the lip swelling, lip teeth and parietal lamella.

Armature: the lip teeth and the parietal lamella together.

Axis: the line drawn through the apex and the umbilicus of the shell.

Bifid: cleft into two lobes, e.g., a lip tooth.

Dished: concave, e.g., an aperture having the lip swelling and the lip teeth slanted inward.

Embryonic whorls: the first 1.4–1.5 whorls of the shell, produced by the embryo inside the egg.

Fulcrum: the callosity inside the last whorl, on the inner wall.

Granule: the small protuberance on the surface of the shell, which does not bear a hair. This term may be used synonymously with papilla; the latter, however, may bear a periostracal hair.

Height: the vertical distance between the lowest point of the aperture and the apex of the shell, measured with the axis held perpendicularly.

Keel: the ridge at the periphery of the whorl.

Lip: the margin of the shell, surrounding the opening of the shell; used synonymously with aperture or peristome. An upper and lower lip can be differentiated.

Lip swelling: the thickening at or near the lip. In the former case, it is marginal, in the latter, receding.

Lip tooth: the protrusion on the lip or lip swelling. It may be marginal or receding.

Lip tooth distance: the distance between the middle point of the tip of the lip tooth and the junction of the lip upon which the tooth rests with the shell.

Papilla: the small protuberance on the surface of the shell, which may bear a periostracal hair. Used synonymously with granule.

Peristome: the margin of the shell that surrounds the opening of the shell. Used synonymously with aperture and lip.

Scale: the small, flat projection of the periostracum.

Sculpture: the pattern of the surface of the shell—the hairs, scales, granules, etc.

Spiral direction: parallel with the direction of the coiling of the shell.

Transverse direction: perpendicular to the direction of the coiling of the shell.

Umbilicus: the opening at the base of the shell, resulting from a loosely coiled columella. Its diameter (width) is measured at the depth of the last whorl. The word umbilicus may stand for the longer term "width of the umbilicus."

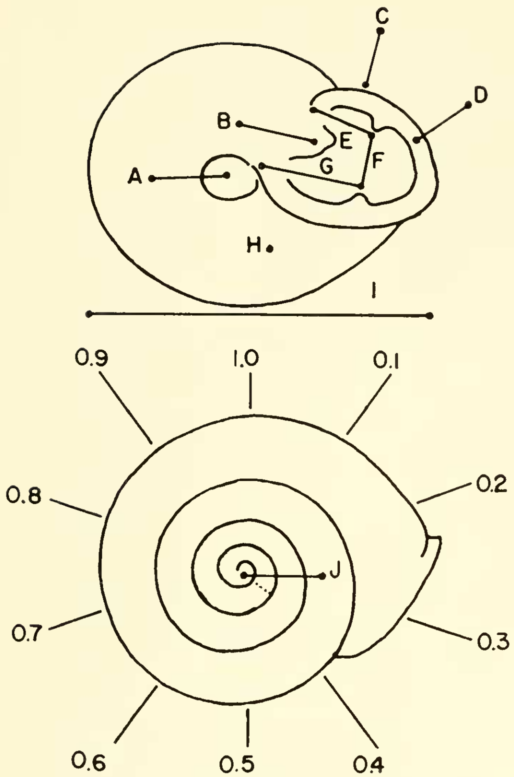

Figure 2. The more important features and measurements of the *Triodopsis* shell. *Above:* figure in side view. A, umbilicus; B, parietal lamella; C, lip, or aperture; D, lip swelling; E, upper lip tooth distance; F, distance between upper and lower lip teeth; G, lower lip tooth distance; H, last whorl; I, width of shell. *Below:* shell in top view. J, embryonic shell, 1.4 whorls. Numbers refer to whorl number; the shell shown has 4.4 whorls.

Whorl: the convolution of the shell. The number of whorls was measured under a binocular microscope, using a circular scale divided into ten parts, with the apex of the shell placed in the center of the circle.

Width: the greatest diameter of the shell across the last whorl. It is approximately perpendicular to the axis of the shell.

Wrinkle: the slight folding of the periostracum; longer than the granule, shorter and slighter than the stria.

The more important terms and measurements are figured below (Fig. 2).

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SYSTEMATIC TREATMENT

Order STYLOMMATOPHORA
Family POLYGYRIDAE
Genus TRIODOPSIS

Type species *Triodopsis lunula* Rafinesque = *Helix tridentata* Say[1]

Triodopsis Rafinesque, 1819, J. Phys. Chim. Hist. Nat. 88: 425.

Menomphis Rafinesque, 1831, Enumeration and account of some remarkable natural objects in the cabinets of Prof. Rafinesque, in Philadelphia, November 1831: 3. Subgenus of *Triodopsis* for *Triodopsis lunula* Rafinesque.

Triodontopsis Agassiz, 1846, Nomenclature Zool., Index Universalis: 378 (emendation of *Triodopsis*).

[1] Rafinesque listed *T. lunula* as the number one species when he described the genus *Triodopsis*. Férussac, 1821, Tabl. Syst. Fam. Limaçons, p. 34, no. 105, put *T. lunula* in the synonymy of *Helix tridentata* Say.

The genus *Triodopsis* belongs to the family Polygyridae, suborder Sigmurethra, order Stylommatophora (Pilsbry, 1940; Zilch, 1960). Its distinguishing features are mainly in the morphology of the reproductive organs. The penis is enveloped by a thin, membranous sheath, which is attached to the penis at the base. There is no stimulator in the penis, or flagellum on it, except for a vestigial flagellum in the subgenus *Cryptomastix*. The shells are small to moderately large, the aperture usually bears two teeth and a lamella; hence the scientific name *Triodopsis* (three-toothed face).

Twenty-two species belong to the genus. Of these, eighteen occur in eastern, and four in western North America. They live in various types of deciduous and mixed pine-deciduous forests, hiding in the litter layer under logs, branches or stones. A few species also occur in the grasslands. The majority of the species prefer the lower elevations, below 1500 feet, but a few may live over 3000 feet. Their food consists of dead leaves or fungi that live on the decaying plant material. The snails are active from early spring to late fall, the cycle being interrupted by temporary aestivations in time of drought. Their life span is several years. In the early spring they lay small batches of eggs a few centimeters below the surface of the ground. The number of eggs in a batch varies from two to twenty, their size, depending upon the species, from two to three and one-half millimeters. At room temperature they hatch in about three weeks. Some of the young grow fast, and reach maturity by the fall, others winter as young and complete their growth the next spring. The latter observations were made in the laboratory, and the possibility exists that the development of the young was slower than in nature. Cleave and Foster (1937) made similar observations on the related form *Mesodon thyroidus* (Say). Grimm, however, stated in a letter that he obtained two generations a year in *Triodopsis fallax*.

The genus is divided into four subgenera: *Triodopsis* (*sensu stricto*), *Xolotrema*, *Neohelix* and *Cryptomastix*. The first three subgenera lack an epiphallus and flagellum, and have only one pilaster in the cavity of the penis; the fourth, *Cryptomastix*, has an epiphallus, flagellum (vestigial), and two pilasters. The first three occur in the eastern parts of the United States and Canada; the fourth is confined to the northwestern United States and Canada. On these grounds, *Cryptomastix* might be considered a separate genus. Because of the subjective nature of classification on supraspecific levels, however, the current generic and subgeneric classification was adopted without any change. My work was oriented toward the specific and intraspecific problems, rather than a generic rearrangement.

The fossil remains of the genus are very scanty. Only a few Pleistocene records are known (Baker, 1920, 1928, 1937; Henderson, 1935; Hubricht, 1961; Leonard, 1952, 1953; Leonard and Frye, 1960; Shimek, 1936). The records include *Triodopsis juxtidens discoidea, T. neglecta vulgata, T. obstricta obstricta, T. o. denotata, T. fosteri fosteri, T. f. hubrichti, T. albolabris* and *T. multilineata*. These are identical or almost identical with the Recent forms. On this basis, it seems probable that most of the species are of Pleistocene or possibly Pliocene origin, and the "young" species developed in the late Pleistocene or Holocene.

Key to Species and Subspecies

The following key can be used to identify adult specimens of *Triodopsis*, except for intergrades. In order to increase its usefulness, dubious cases are keyed out twice. Thus, *T. c. complanata*, which may have small lip teeth or almost none, is keyed out among both the tooth-bearing and the toothless forms.

1a	Shell umbilicated	2
b	Shell imperforate	28
2a	Embryonic shell smooth or striated; eastern United States	3
b	Embryonic shell with striae and often also with granules; Pacific Coast	24

3a Umbilicus very narrow and partially covered by reflected edge of peristome 4
b Umbilicus narrow to wide, not covered by reflected edge of peristome 5
4a Shell width 17–26 mm, sculpture of triangular scales; lower lip swelling reaches columella; hybridizes with *o. obstricta*; from Vermont to Michigan and Tennessee ..... *o. denotata*, p. 206
b Shell width 10–11 mm; no triangular scales; lower lip swelling terminates shortly before columella; restricted to North Carolina ..... *soelneri*, p. 204
5a Lip teeth absent 6
b Lip teeth present 9
6a Aperture auricular, lip swelling thin, peristome sharp; intergrades with *f. obsoleta*, grade B; lower areas of the southeastern Coastal Plain, from Maryland to Georgia ..... *f. obsoleta*, grade A, p. 187
b Aperture oval-triangular, lip swelling thin or thick, peristome swollen, at least in some places 7
7a Shell width 9–13 mm; Piedmont region of Virginia ..... *burchi*, p. 160
b Shell width 17–27 mm 8
8a Shell width 26–27 mm, umbilicus very wide all the way; restricted to northern West Virginia ..... *c. platysayoides*, p. 159
b Shell width 17–24 mm, umbilicus somewhat narrower at the early whorls and widens out later; Kentucky, Tennessee, and adjoining regions ..... *c. complanata*, p. 157
9a Parietal lamella points at or below upper lip tooth when looking at the shell from below 10
b Parietal lamella points above upper lip tooth when looking at the shell from below 11
10a Lip swelling slightly receding, peristome sharp and flat; lip teeth moderate to large; from Ontario to Michigan, Georgia and Alabama ..... *tridentata*, p. 151
b Lip swelling marginal, lip swollen, lip teeth usually small or lacking; *burchi* or *complanata*, go back to 7
11a Upper lip swelling slants inward, parietal lamella often very large; these features may not be clear, however; check description and figures of *rugosa* and *fulciden* 12
b Upper lip swelling does not slant inward, parietal lamella rarely large 13
12a Shell width 10–16 mm; West Virginia and neighboring areas ..... *rugosa*, p. 161
b Shell width 8–9 mm; confined to the Piedmont region of North Carolina ..... *fulciden*, p. 164
13a Upper lip tooth distance roughly the same as lower lip tooth distance 14
b Upper lip tooth distance is considerably greater than lower lip tooth distance 16
14a Shell and aperture depressed, umbilicus moderately wide, shell often smooth and shiny; Ohio and Mississippi valleys, from Ohio to Missouri ..... *j. discoidea*, p. 171
b Shell and aperture not depressed, umbilicus narrow or very narrow, shell never smooth and shiny 15
15a Umbilicus narrower, coiling of shell tighter and parietal lamella larger; hybridizes with *j. juxtidens*; New Jersey and adjoining Pennsylvania and New York, also Virginia ..... *j. stenomphala*, p. 169
b Umbilicus wider, coiling of shell looser and parietal lamella smaller; hybridizes with *j. stenomphala*; eastern seaboard from Vermont to Georgia, west to West Virginia ..... *j. juxtidens*, p. 165
16a Lip teeth and parietal lamella large, and thus obstruct the aperture to a considerable degree 17
b Lip teeth and parietal lamella small or moderately large, and thus do not obstruct the aperture significantly 19
17a Fulcrum present, umbilicus narrow but suddenly widening at the last whorl 18
b Fulcrum absent, umbilicus wide; Appalachian Mountains in West Virginia and Virginia ..... *fraudulenta*, p. 181
18a Lip swelling marginal, peristome swollen; hybridizes with *c. cragini*; Texas ..... *c. copei*, p. 199
b Lip swelling slightly receding, peristome sharp; intergrades with *f. obsoleta* and *f. alabamensis*; Blue Ridge Mountains, and the higher regions of the southeastern coastal plain, from Pennsylvania to Georgia and Tennessee ..... *f. fallax*, p. 184
19a Umbilicus wide 20
b Umbilicus narrow or medium wide, or narrow at the beginning and widening suddenly at the last whorl 21
20a Shell width 12–20 mm, coiling of shell moderately tight, umbilicus wide; intergrades with *n. neglecta*; from Ontario to Wisconsin, North Carolina and Tennessee ..... *n. vulgata*, p. 175
b Shell width 10–13 mm, coiling very tight; intergrades with *n. vulgata*; Ozark area ..... *n. neglecta*, p. 178
21a Last whorl, measured behind the aperture, is more than one and one-half times wider than the penultimate one, when looking at the shell from above;

lower lip tooth located close to columella; isolated spots in North Carolina, Pennsylvania and Ohio .... *pendula*, p. 180

b Last whorl less than one and one-half times wider than the penultimate one, lower lip tooth near middle of lower lip 22

22a Aperture auriculate, peristome sharp, whorl-width ratio 0.39–0.53; intergrades with *f. obsoleta*, grade A, and *f. fallax*; hybridizes with *f. alabamensis*; southeastern Coastal Plain from Maryland to Georgia .... *f. obsoleta*, grade B, p. 187

b Aperture square to oval, peristome often swollen, whorl-width ratio 0.47–0.68 23

23a Shell width 8–13 mm, number of whorls 4.9–7.0, upper lip tooth slightly receding; extensively hybridizes with *f. fallax* and *f. obsoleta*; Alabama, and an isolated spot in Virginia .... *f. alabamensis*, p. 193

b Shell width 7–11 mm, number of whorls 4.3–5.5, upper lip tooth definitely receding; hybridizes with *c. copei*; from eastern Kansas to Texas and Louisiana .... *c. cragini*, p. 201

24a Shell 6.6–6.8 mm wide, very tightly coiled; no lip teeth; Pacific Coast from Vancouver Island to Oregon .... *germana*, p. 231

b Shell larger than 8.6 mm, less tightly coiled, lip teeth usually present 25

25a Shell width over 12 mm, lip teeth and parietal lamella small or absent (although lip swelling may be thick) 26

b Shell width below 11.3 mm, lip teeth and parietal lamella medium to large 27

26a Shell width 19–26 mm, lower lip tooth, or the swelling that replaces it, located near columella; west of the Cascade Range, in Washington and Oregon .... *devia*, p. 230

b Shell width 12–19 mm, lower lip tooth, or the swelling that replaces it, located in middle of lower lip; hybridizes with *m. harfordiana*; east of the Cascade Range, in Oregon, Idaho and Montana .... *m. mullani*, p. 223

27a Shell width 8.6–10.1 mm, umbilicus very wide; hybridizes with *m. mullani*; restricted to the Snake River valley in Idaho .... *m. hardfordiana*, p. 227

b Shell width 10.1–11.3 mm, umbilicus narrow and partly covered by reflected edge of peristome; central and northern Idaho .... *sanburni*, p. 229

28a Embryonic shell with striae and often also with granules; Pacific region; *germana*, *devia*, *mullani* or *sanburni*, go back to 24

b Embryonic shell smooth or striated; eastern United States and Canada 29

29a Fossil; shell width 19–25 mm, lip teeth and parietal lamella small; Illinois .... *f. hubrichti*, p. 212

b Recent 30

30a Sculpture of fine spiral lines with extremely fine transverse lines between them; Mississippi and Missouri valleys, from Iowa to Louisiana .... *f. fosteri*, p. 210

b Sculpture different 31

31a Lip teeth and parietal lamella small to large 32

b Lip teeth and parietal lamella usually absent, very small if present 33

32a Sculpture of triangular scales, last whorl rounded or bluntly angular at the periphery; hybridizes with *o. obstricta*; from Vermont to Michigan and Tennessee .... *o. denotata*, p. 206

b Sculpture of short wrinkles, last whorl sharply angular or keeled at the periphery; hybridizes with *o. denotata*; Kentucky and Tennessee .... *o. obstricta*, p. 205

33a Shell banded, rarely uniformly brown-red or horn colored; from Ohio to Minnesota and Kansas .... *multilineata*, p. 219

b Shell unicolored 34

34a Shell width 17–20 mm, height 8–12 mm, lip swelling thin; Ozarkian area, from Kansas to Louisiana .... *divesta*, p. 222

b Shell width 19–42 mm, height 11–31 mm, lip swelling medium to very thick 35

35a Lip swelling very thick, small parietal lamella present, shell often flat; from Quebec to Pennsylvania and North Carolina .... *dentifera*, p. 218

b Lip swelling moderately thick or very thick, parietal lamella only exceptionally present, shell flat to very high 36

36a Shell with faintly visible grid formed by transverse wrinkles and spiral lines, or smooth and shiny; flatter; intergrades with *a. albolabris* and *a. major*; from Minnesota to Arkansas .... *a. alleni*, p. 216

b Sculpture of the same elements but much coarser, shell higher 37

37a Shell 20–36 mm wide, less globose; intergrades with *a. alleni* and *a. major*; from Quebec to Michigan and Tennessee .... *a. albolabris*, p. 213

b Shell 27–42 mm wide, globose; intergrades with *a. albolabris* and *a. alleni*; North Carolina to Alabama .... *a. major*, p. 214

Subgenus *TRIODOPSIS* sensu stricto

The nominate subgenus is characterized by its small or moderately large, umbilicated shell, and the presence of two lip teeth and a parietal lamella in the aperture. Anatomically, the description of the genus fits the subgenus well. Subgenera *Xolotrema* and *Neohelix* are separated from *Triodopsis* mainly on the basis of shell characters, *Cryptomastix* on the basis of anatomical features and distribution.

The subgenus contains 12 of the 22 species that belong to the genus. Many of the species exhibit great complexity, which makes the classification difficult but provides rich material for evolutionary studies. The species can be grouped in five natural, hence easily recognizable, species complexes. These are: *tridentata*, *rugosa*, *juxtidens*, *fraudulenta*, and *fallax*.

The *tridentata* Complex

The *tridentata* complex comprises three closely related forms: *tridentata*, *complanata* and *burchi*. Of these, *tridentata* and *complanata* are undoubtedly distinct species, while *burchi*, a diminutive form of *complanata*, may be either a distinct species or a subspecies.

The *tridentata* complex shows a close relationship to the *rugosa* complex.

Triodopsis tridentata (Say)
Plate I: 1–8

Helix tridentata Say, 1817, Nicholson's Encyclopedia, 1st American Edition, article "Conchology." "Middle States." Neotype designated by Pilsbry (1940: 790, fig. 474a). Type locality: northern edge of Philadelphia, Montgomery County, Pennsylvania. Neotype and paratypes ANSP 105972.

Triodopsis lunula Rafinesque, 1831, Enumeration and account of some remarkable natural objects in the cabinets of Prof. Rafinesque, in Philadelphia, November 1831: 3. "Kentucky." Types not examined.

Polygyra tridentata edentilabris Pilsbry, 1894, Nautilus, 7: 140. "Cumberland Mountains." Type ANSP 57255.

Definition. The name *tridentata*, as used here, applies to *Triodopsis t. tridentata* and *t. edentilabris* of earlier authors.

Description. Shell width 12.3–20.7 mm; height 5.5–11.0 mm; height to width ratio 0.43–0.57; umbilicus 2.0–4.3 mm; umbilicus to width ratio 0.14–0.24; embryonic whorls 1.4–1.5, with striae and granules below suture, smooth elsewhere; striation more pronounced on subsequent whorls; three wide, low striae per millimeter on last whorl; space between striae always granulated; granules numerous below suture and in umbilical region; aperture oval-triangular; lip swelling marginal; lip teeth moderately developed; lower tooth located at variable distance from juncture of lower lip with shell; parietal lamella slightly angular, pointing at or slightly below upper lip tooth.

Distribution. *Triodopsis tridentata* occurs in southeastern Canada and eastern and central United States, from Ontario south to Alabama and west to Iowa (Fig. 3). It is entirely absent from the eastern Kentucky-Tennessee area, however, and is there replaced by the related species *Triodopsis c. complanata*. This interesting phenomenon will be discussed in some detail below.

There is, in the ANSP collection, a single specimen of *T. tridentata* (ANSP 57231), collected by A. D. Brown in "Adams County, Missouri." This record appears to be erroneous, since no such county exists in Missouri, and the specimen, judging from its appearance, must have come from farther north.

The *measured material* comes from the following localities. *New Hampshire*: Grafton (2 samples) and Merrimack counties (MCZ). *Vermont*: Orleans, Chittenden, Addison, and Rutland counties (MCZ). *New York*: Albany, Herkimer, Madison, Onondaga, Niagara, Ulster, and Richmond counties (MCZ). *Ontario*: Wellington County (MCZ). *Michigan*: Oakland, Washtenaw, Ingham, and Calhoun (2 samples) counties (MCZ). *Massachusetts*: Hampden and Berkshire counties (MCZ).

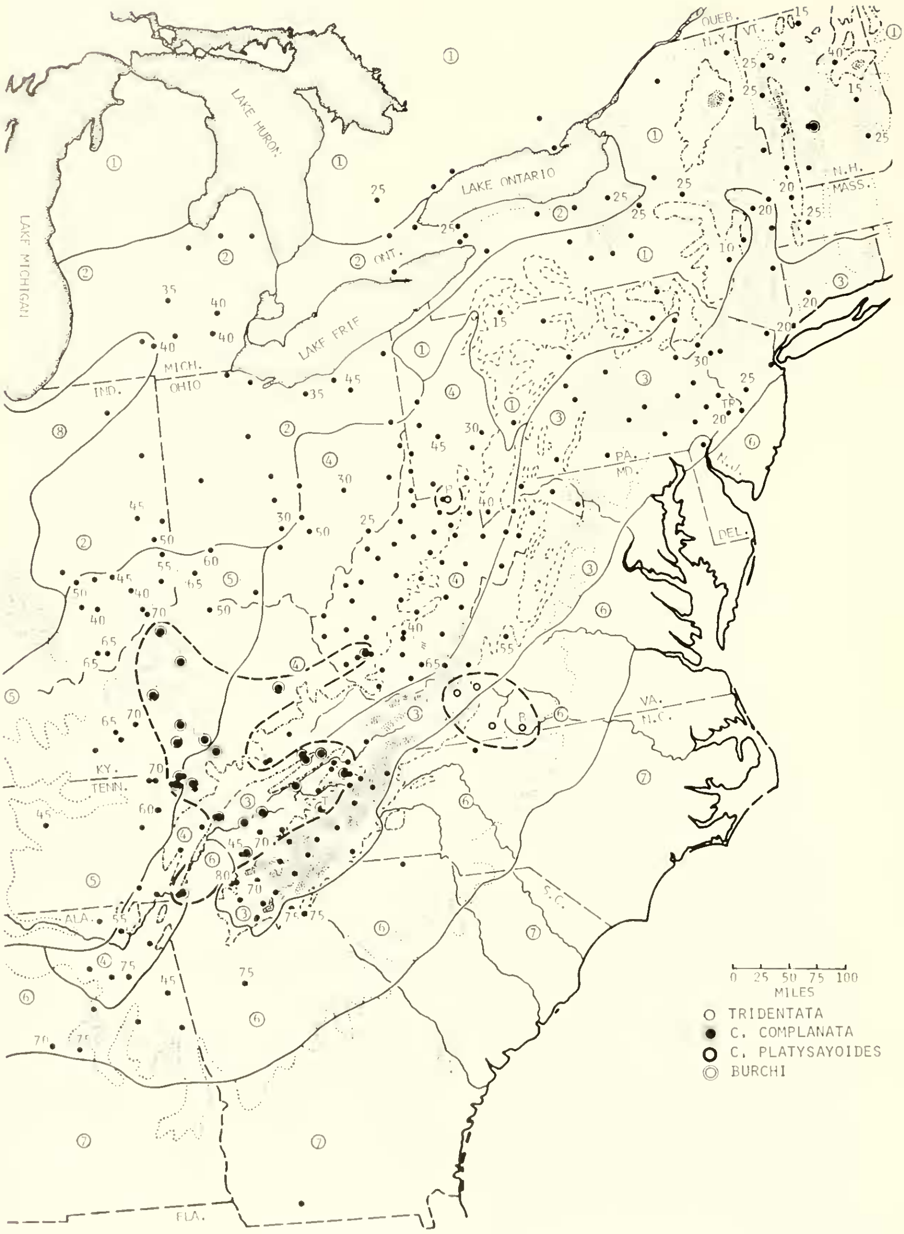


Figure 3. Distribution of *Triodopsis tridentata*, *complanata*, and *burchi* and the geographic variation of the character index in *tridentata*. One record of *tridentata* from Illinois and another from Iowa have been omitted. Thick, dashed line surrounds the range of *c. complanata*, *c. platysayoides*, and *burchi*. B, type locality of *burchi*; C, *c. complanta*; P, *c. platysayoides*; T, *tennesseensis*, considered synonymous with *c. complanata*; TR, *tridentata*. Numbers without a circle are mean values of samples in character index; they range from 15 in the north to 80 in the south. Numbers encircled refer to forest types; one, northern hardwood forest; two, beech maple; three, oak-chestnut; four, mixed mesophytic; five, western mesophytic; six, oak-pine; seven, southeastern evergreen; eight, oak-hickory forest; nine, prairie or grassland; ten, maple basswood forest (terminology after Braun, 1950). Elevation: . . . . . . 500-foot contour line; • — • — • 1500 foot; ⁙ area over 3000 feet. Thin dashed lines mark state boundaries.

Connecticut: Fairfield County (2 samples, MCZ). *New Jersey*: Mercer County (MCZ). *Pennsylvania*: Northampton, Philadelphia, Dauphin, McKean, Indiana, and Allegheny counties (MCZ); Lee County (JV). *Maryland*: Garrett County (MCZ). *West Virginia*: Fayette and Mercer counties (CM). *Ohio*: Summit, Lorain, Washington, Muskingum, Hocking, Pickaway, and Hamilton counties (MCZ). *Indiana*: Fayette, Henry, Franklin, Dearborn, Jennings, Bartholomew, Jackson, Monroe, Harrison, and Crawford counties (MCZ). *Kentucky*: Pendleton, Trimble, Hart, and Edmondson counties (MCZ); Bell County (JV). *North Carolina*: Avery, Yancey, Henderson, Swain, and Cherokee counties (MCZ). *Tennessee*: Sullivan, Sevier, Monroe, Polk, Clay, Cumberland, Putnam, Dickson, and Hamilton counties (MCZ). *Georgia*: Stephens, Habersham, and Fulton counties (MCZ). A total of 80 samples, 1–15 specimens each, 395 specimens altogether.

Ecology. Triodopsis tridentata occurs in northern hardwood, mixed deciduous, and mixed oak-pine forests (Fig. 3, phytogeographic terms after Braun, 1950). In New York and New Jersey it approaches sea level. In the Appalachian Mountains, specifically in the Roan Mountains, Carter County, Tennessee, it ascends to as high as 4000–5000 feet. The latter habitat assumedly still lies in the oak-chestnut forests, which reach up to 4500–5000 feet (Braun, 1950: 206).

Triodopsis tridentata lives in the litter layer of the forests, under fallen logs or other kinds of shelter. Its food is supplied by decaying leaves and the fungi that grow on them. Its ecological niche thus seems to be very similar to that of the related forms *T. c. complanata*, *j. juxtidens* or *f. fallax*. It is probably because of this similarity that *tridentata* cannot coexist with any of these forms. Should it invade, competition would ensue, which eventually would lead to the exclusion of one or the other (exclusion principle of Hardin, 1960). This may explain the distributional pattern (replacement) of these forms (Figs. 3, 9, 15). The exclusion principle seems also to be at work when *tridentata* overlaps (geographically) other forms of *Triodopsis*, such as *c. platysayoides* or *j. discoidea*. The overlapping forms do not occur together, *tridentata* being confined always to the relatively drier, and the other two the relatively more moist habitats within the zone of overlap. In these cases, then, exclusion led to ecological separation of the (once) competing forms.

Variation. Aperture: Four grades of aperture can be distinguished, based on the shape of the aperture and development of the lip swelling and lip teeth. In grade A the aperture is oval-triangular, the lip swelling moderately and uniformly thick along its entire length and the lip teeth moderately large (Plate I). The aperture of grade B also is oval-triangular, but the lip swelling is somewhat thicker, and the lip teeth larger. In grade C the outer contour of the aperture is oval-triangu'ar. The inner contour of the upper lip runs parallel with the outer contour, but that of the lower lip does not, because the lower lip swelling is higher in the middle than in the corners, thus forming a straight, ledge-like structure; sometimes the upper lip is swollen instead of the lower. The lip swelling generally is thicker than in grade B, and the lip teeth are larger. In grade D the lip swelling is the thickest, the lip tooth the largest, and both the upper and lower lip swellings are straight, like the lower lip swelling of grade C. The four grades form a continuous series, although A-B and C-D are more similar to each other than is B to C.

Similar aperture series occur in *T. fallax*, *T. copei*, *T. mullani*, *T. rugosa*, and *T. fraudulenta*. In all cases except that of *copei* the grades with the heavier armature occupy higher elevations than do those with the lighter armature. This seems to indicate that the heavy armature is an adaptation to

TABLE I

CHART FOR COMPUTING CHARACTER INDEX IN *TRIODOPSIS TRIDENTATA*. METHOD OF CALCULATION: A SPECIMEN WITH A SHELL WIDTH OF 20.5 MM, AN UPPER TOOTH TO LOWER TOOTH RATIO OF 1.10, AND AN APERTURE GRADE D WAS SCORED (100 + 70 + 30)/2 = 100, THE AVAILABLE MAXIMUM SCORE.

SCORE	SHELL WIDTH	UPPER TO LOWER TOOTH RATIO	APERTURE GRADE	
0	12.3–12.7	0.69–0.72	A	Northern
5	12.8–13.1	0.73–0.74		populations
10	13.2–13.5	0.75–0.77	B	↑
15	13.6–13.9	0.78–0.80		
20	14.0–14.2	0.81–0.83	C	
25	14.3–14.6	0.84–0.86		
30	14.7–14.9	0.87–0.89	D	
35	15.0–15.3	0.90–0.92		
40	15.4–15.6	0.93–0.95		
45	15.7–16.0	0.96–0.98		
50	16.1–16.3	0.99–1.01		
55	16.4–16.7	1.02–1.04		
60	16.8–17.1	1.05–1.07		
65	17.2–17.5	1.08–1.09		
70	17.6–17.9	1.10–1.13		
75	18.0–18.3			
80	18.4–18.7			
85	18.8–19.1			
90	19.2–19.6			↓
95	19.7–20.1			Southern
100	20.2–20.7			populations

high elevations, but its specific significance is, as yet, unknown (p. 239).

The geographic variation of the aperture is basically clinal, since in the northern parts of the range grade A individuals predominate, in the middle regions grade B, and in the southern, grade C. The grade D specimens, however, do not fit into this pattern, since they occur near the center of the range, instead of in the southern end, as might be expected. This seemingly anomalous distribution makes sense only if we consider that D is a mountain-adapted form, and that the area southeast of the center of the range is mountainous. Thus, it is natural that altitudinal variation is superimposed upon the basically latitudinal, clinal variation.

Measured characters: The shell width (size) is statistically correlated with shell height, umbilicus, and, to a degree, with the ratio of the upper lip tooth distance to the lower lip tooth distance. The species shows an overall size increase in its range from north to south. In the southern half of the range, however, the variation is irregular; we cannot, therefore, speak of a true cline in size.

The height to width ratio and umbilicus to width ratio vary irregularly throughout the entire range. The upper tooth to lower tooth ratio shows a slight and gradual increase from north to south. This ratio is, to an extent, correlated with the aperture grades, grade A specimens having lower, and grade B, C and D specimens increasingly higher ratios. The correlation is not a perfect one, however, because grade B, on the basis of overall similarity, is closer to grade A than to grade C, but according to the upper tooth to lower tooth ratio, it appears to be closer to C than to A.

Character index: The character index was calculated with the aid of the chart shown below (Table I). The mean values of populations in the character index show a gradual increase from north to south (Fig. 3). A relatively sharp character gradient occurs only in the area where the valleys of the Holston and French Broad rivers, and the Yadkin and Catawba rivers cut deeply into the ranges of the Appalachians. These valleys may be responsible for the existence of the gradient, because they probably act as partial barriers to the gene flow along the Appalachian ranges.

The range of variation in the character index is of the same order of magnitude in all measured populations (Fig. 4). Note that in this figure it is not the actually observed ranges which are compared, but the mean expected ranges of hypothetical populations. The observed ranges cannot be directly compared, because they belong to populations of different size, and the range of variation tends to vary with the size of the population. Therefore, we must calculate how large the range of variation would be if the populations were all of the same

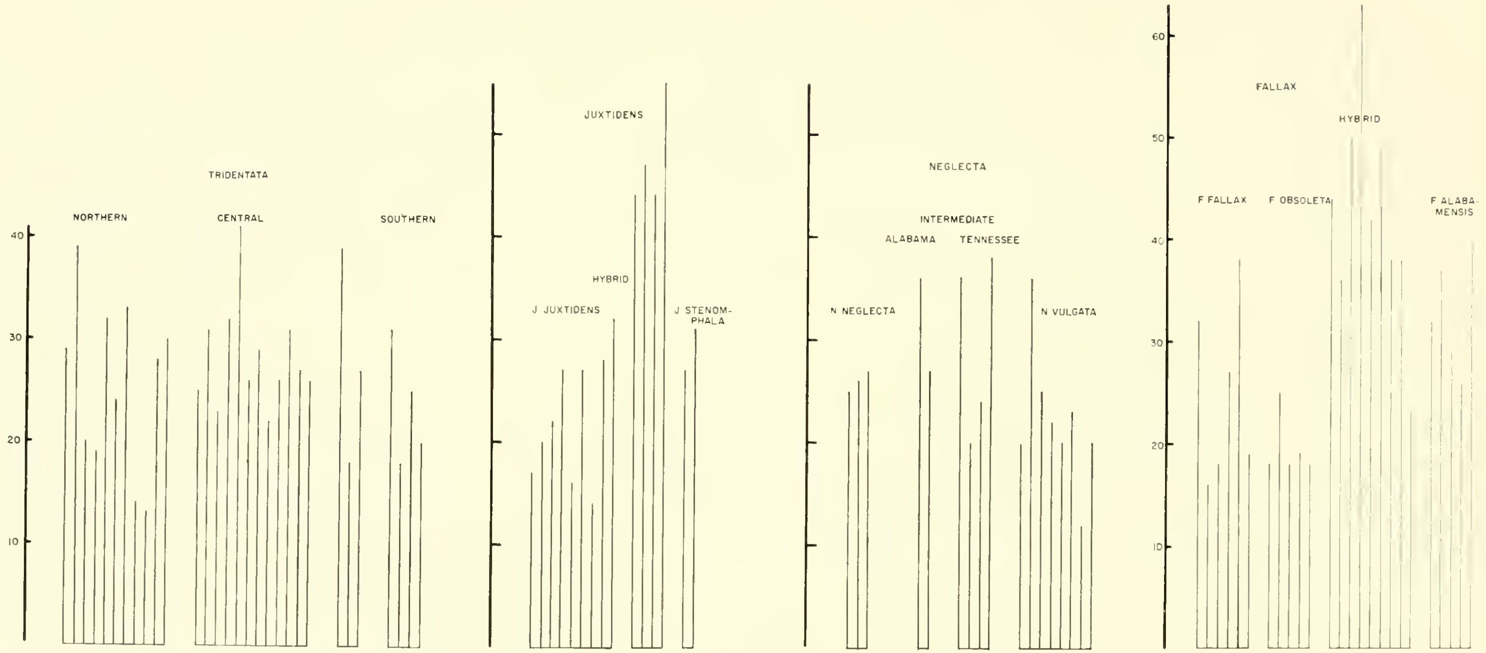


Figure 4. Range of variation in samples of *Triadopsis tridentata, juxtidens, neglecta,* and *fallax*. The range is calculated with the method described on p. 156. Scale in character index units. The range is considerably greater in the hybrid samples than in most other samples. The samples of *f. alabamensis* also have a somewhat wider range than those of *f. fallax* or *f. obsoleta.*

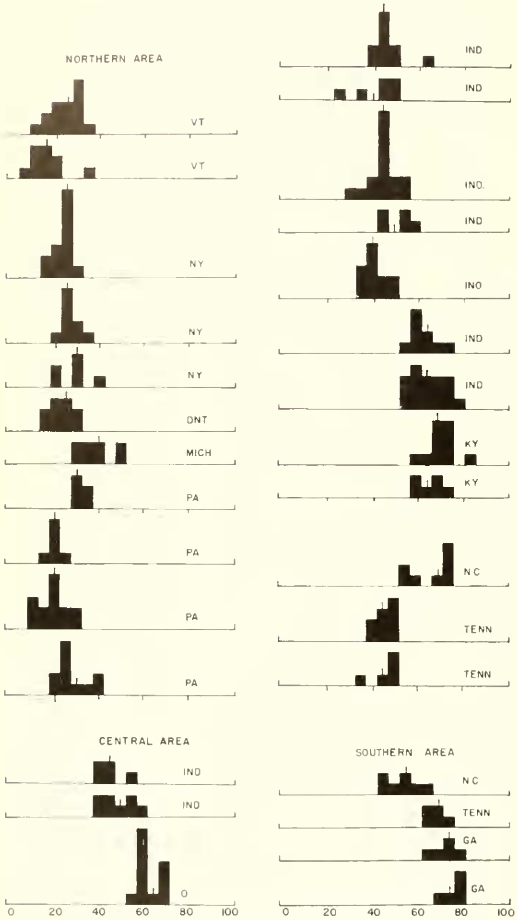


Figure 5. Character index histograms of samples of *Triodopsis tridentata.* Short line on top of column indicates mean value of samples. All histograms are normal or slightly skewed. The abbreviations stand for the states where the samples have been collected. Scale in character index units.

size. This can be done by using Simpson's method (1941), which, briefly, consists of multiplying the standard deviation of the actual populations by an appropriate factor, e.g., 6.48 if N = 30 is selected as the standard population size. The hypothetical ranges thus obtained can be directly compared. These ranges for all *tridentata* populations are of the same order of magnitude, which indicates that the variation of the species is primary. (Should secondary intergradation be the case, the intergrading populations would be expected to show greater variation than the others.) This conclusion is supported by the fact that the distribution curves of the populations in the character index are normal (Fig. 5), whereas those of hybrid populations are skewed (see histograms of *T. juxtidens* and *T. fallax*, Figs. 11 and 18).

Systematics. Triodopsis tridentata of Pilsbry (1940) and most contemporary authors is an oversized, artificial taxon. It is said to consist of six subspecies, but, in my opinion, four of these should be excluded and the other two should be combined. Those to be excluded are *T. t. complanata, t. tennesseensis, t. juxtidens,* and *t. discoidea*; those to be combined are *t. tridentata* and *t. edentilabris. Triodopsis t. edentilabris* (Pl. I, figs. 5, 6) of the "Cumberland Mountains" differs from *tridentata* in lacking the lip teeth, although the lip swelling is normally developed, and in having more obese whorls and a shorter and higher aperture. It must be admitted that these specimens are "recognizably different" from *tridentata.* But toothless specimens, which approach *edentilabris,* occur in many populations of *tridentata.* Also, it must be kept in mind that there are only three known specimens of *edentilabris*; thus, we cannot expect to find much intergradation. For these reasons, I prefer to consider *edentilabris* a synonym of *tridentata.* The distributional data allow this conclusion, since *edentilabris* is only known from a single locality somewhere in the Cumberland Mountains, which lie within the range of *tridentata.*

The difference between the northern and southern populations of *tridentata* is as great as that between different species. It may therefore seem desirable to separate these populations on the subspecies level. Because, however, the two populations intergrade without a convenient break which would allow a natural division between them, it seems better to keep them in a single taxon.

Evolutionary relationships. Triodopsis *tridentata* is probably the stock from which developed the related species *T. complanata* and *T. burchi.* It has a three-toothed aperture and a striated shell, whereas *complanata* and *burchi* have reduced dentition and smooth or striated shells. The *tridentata* features can be considered primitive, because they are common in many unspecialized species of *Triodopsis.* The features of *complanata* and *burchi* are presumably more advanced, because they occur in a few species which may well be ecologically specialized.

Summary. (1) *Triodopsis tridentata* is a monotypic species. It corresponds to the former *T. tridentata tridentata,* to which the former *t. edentilabris* is added as a synonym.

(2) *Triodopsis tridentata* is distributed in eastern North America from Ontario south to Alabama and west to Iowa. In eastern Kentucky and eastern Tennessee it is replaced by the related form *T. c. complanata.*

(3) *Triodopsis tridentata* lives in the litter layer of mixed deciduous and oak-pine forests, ranging from low to high elevations. It shows habitat exclusion with *T. c. complanata, j. juxtidens,* and *f. fallax,* and with *T. c. platysayoides* and *j. discoidea.*

(4) The geographic variation of certain features is clinal, that of others irregular. There is a continuous intergradation between the extreme northern and the extreme southern populations in combined character index. The range of variation is essentially the same in all populations.

(5) *Triodopsis tridentata* is probably ancestral to *T. complanata* and *T. burchi.*

Triodopsis complanata (Pilsbry)
Triodopsis complanata complanata (Pilsbry)

Plate I: 9–11

Polygyra tridentata var. *complanata* Pilsbry, 1898, Nautilus 12: 22. Burnside, Pulaski County, Kentucky. Type ANSP 71399.

Polygyra tridentata var. *tennesseensis* Walker and Pilsbry, 1902, Proc. Acad. Nat. Sci. Philadelphia 54: 422. Foot of the high bluffs on south side of French Broad River below Paint Rock, Madison County, North Carolina. Type ANSP 84022.

Definition. Triodopsis c. complanata combines the former *T. tridentata complanata* and *t. tennesseensis.*

Description. Shell width 16.7–23.3 mm; height 8.0–10.6 mm, height to width ratio 0.40–0.54; umbilicus 2.9–6.0 mm, umbilicus to width ratio 0.17–0.26; embryonic whorls 1.4–1.5, with dense striae and long, transverse granules; two subsequent whorls almost exclusively with granules, then striation becoming more pronounced, 3–4 low to moderately high striae per millimeter on last whorl; intervals between striae with granules; incised spiral lines appearing after breakage; aperture oval-triangular; lip swelling well developed, marginal or sometimes bulging in vicinity of upper lip tooth; lip teeth very small, sometimes only bare traces, rarely moderately large; upper lip tooth rather close to juncture of upper lip with shell; distance between lip teeth nearly as great as distance of upper lip tooth from juncture of upper lip with shell; parietal lamella short, pointing well below upper lip tooth.

Differential diagnosis. Triodopsis c. complanata is best distinguished from *T. tridentata* on the basis of apertural features. The lip swelling is very close to the edge of the aperture, so that the latter appears swollen, especially in the vicinity of the upper lip tooth. The lip teeth are small, sometimes barely discernible, rarely moderately large; the distance between the upper and lower lip teeth is nearly as great as the distance between the upper lip tooth and the juncture of the upper lip with the shell (Fig. 6). The parietal lamella is short and straight, corresponding to the distal portion of the parietal lamella of *tridentata,* and when looking at the shell from below, points well below the upper lip tooth. In *tridentata,* the lip swelling is moved back slightly from the peristome, so that the latter is relatively sharp. The lip teeth are medium to well developed; the distance

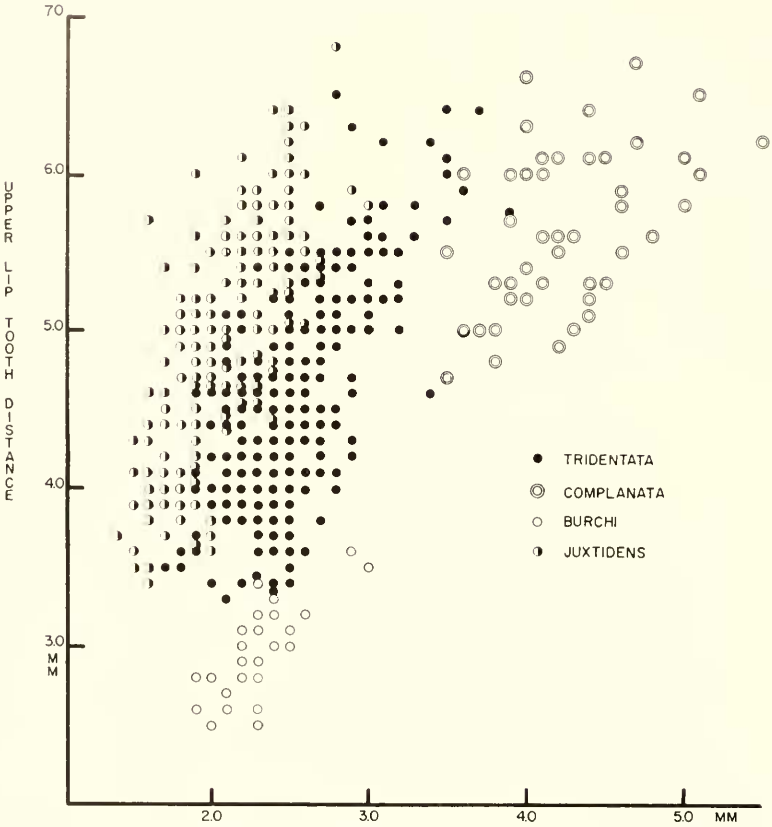


Figure 6. Scatter diagram of upper lip tooth distance (ordinate) versus distance between upper and lower lip teeth (abscissa) in *Triodopsis tridentata, complanata, burchi,* and *juxtidens*. Each dot represents one or more specimens. Scale in millimeters.

between the upper and lower lip teeth is definitely smaller than the distance between the upper lip tooth and the juncture of the upper lip with the shell. The parietal lamella is long and slightly angular; it points to or slightly below the upper lip tooth. Further differences are in the shell. *Triodopsis c. complanata* is larger and flatter than *tridentata*, although there is a wide overlap. Also, *c. complanata* is sometimes smooth and glossy, whereas *tridentata* is always striated. Striated *c. complanata* shells with relatively well-developed teeth may be difficult to separate from *tridentata*.

Pilsbry emphasizes the similarities between *c. complanata* and *j. discoidea*, saying that, "Except in the widely separated and weaker lip teeth it [*c. complanata*] resembles *T. t. discoidea* . . . ." (1940: 801). I believe that Pilsbry was describing only a superficial similarity caused by the glossiness of the shell. *Triodopsis t. discoidea* (*j. discoidea*) in reality belongs to quite another species complex, *juxtidens*.

Distribution. Triodopsis c. complanata occurs in Kentucky, Tennessee, and the adjoining regions of West Virginia, Virginia, and North Carolina (Fig. 3). It is remarkable that the related species, *T. tridentata*, which occurs from Ontario south to Alabama, is largely absent from this area. This replacement will be discussed in the section on ecology.

In the MCZ collection there is a specimen allegedly from Mt. Ascutney, Windsor County, Vermont (MCZ 49268, from the Stearns Collection). This locality is so far outside the normal range that its correctness is questionable.

The *measured material* comes from the following localities (Fig. 3). *West Virginia*: Logan County (2 samples, JV). *Virginia*: Scott County (MCZ). *Kentucky*: Henry, Marion, Casey, Pulaski, and Russell counties (MCZ); Pulaski (2 samples), Breathitt and McCreary counties (ANSP). *Tennessee*: Washington, Monroe, Hancock, and Overton counties (MCZ); Hamblen, Knox, Morgan, and Hamilton counties (ANSP). *North Carolina*: Madison County (ANSP). A total of 22 samples, 1–11 specimens each, 65 specimens altogether.

Ecology. Triodopsis c. complanata occurs in oak-chestnut, mixed mesophytic, and western mesophytic forests, between 500 and 1500 feet elevation (Fig. 3). The forest boundaries do not coincide with the subspecies borders. Nor do the contour lines, except in the eastern part of the range, where the subspecies border closely follows the 1500 foot line.

Triodopsis c. complanata is absent from the territory of *T. tridentata* nearly everywhere (Fig. 3). The apparent reason is that the two species, which are of similar size and also of similar living habits, compete with each other; given enough time, one will exclude the other. This phenomenon of exclusion (Hardin, 1960) provides an explanation of the geographical replacement of *tridentata* with *c. complanata*, mentioned above.

Variation. The sculpture is correlated with the habitat to the extent that smooth and shiny shells only occur in places near water, whereas striated shells occur both near and far away from water. It is possible that the smooth sculpture is caused by the high degree of humidity of the habitat (Rensch, 1932), but there are no experimental data available.

The measured characters are statistically correlated with each other; their geographic variation is irregular.

Systematics. Triodopsis c. complanata as defined in this paper combines the former *T. tridentata complanata* and *t. tennesseensis.* The combination of these forms is justified on morphological and distributional grounds. The former is said to have a smooth shell, the latter a striated one. In fact, however, many specimens occur with finely striated shells which may belong to either of the two "subspecies." The two forms do not have separate ranges either; instead, the striated form surrounds and "overlaps" the smooth form, which occurs in a very restricted area. Thus, to consider the smooth population a subspecies would amount to calling an ill-defined and localized form a subspecies, which, I believe, should be avoided. The irony of the situation is that the name of the more widely distributed form, *tennesseensis*, is newer than that of the restricted form, *complanata*, and therefore the former must be considered a synonym, and the latter the valid name.

Triodopsis c. complanata must be specifically separated from *T. tridentata.* It overlaps and in a few places coexists with *tridentata* without interbreeding, which proves that it is specifically distinct from that species.

Triodopsis complanata platysayoides (S. T. Brooks)

Polygyra platysayoides Brooks, 1933, Nautilus 46: 54. Cooper's Rock, Monongalia County, West Virginia. Type not seen.

Definition. Triodopsis c. platysayoides is the former *T. platysayoides*.

Description and differential diagnosis. Triodopsis c. platysayoides differs from *c. complanata* in the larger dimensions of the shell and the more cylindrical umbilicus. The width of the shell is 26.5 mm (16.7–23.5 mm in *c. complanata*); height 10.5

mm, height to width ratio 0.40; umbilicus 60 mm, umbilicus to width ratio 0.23 on the only specimen which was fit for taking measurements. The shell is finely striated and shiny. The lip teeth are absent, but the lip swelling is somewhat thicker in those places where the lip teeth would occur. The umbilicus is almost as wide at the beginning as at the later whorls; thus it is more cylindrical than the umbilicus of *c. complanata.*

Distribution. Triodopsis c. platysayoides is a geographical isolate of *c. complanata.* It is known only from a single locality in northern West Virginia, Cooper's Rock State Park in Monongalia County, about 150 miles away from the area of *c. complanata* (Fig. 3). Two samples, 4 specimens altogether, have been studied.

Ecology. The habitat in which *T. c. platysayoides* lives is a deep canyon of the Cheat River, between 1000 and 1300 feet elevation. We failed to find the snail on the hills which surround the canyon. Only *T. tridentata* was found on these hills. This arrangement seems very similar to that found between *T. c. complanata* and *T. tridentata*, and thus it seems likely that ecological exclusion is also involved here.

Variation. Because of the extremely small population, there is no variation to speak of.

Systematics. Triodopsis c. platysayoides is usually ranked as a full species in the contemporary literature. It is more likely, however, that it is conspecific with *T. c. complanata*, because they are morphologically remarkably similar. The similarity is so great, indeed, that, should populations be found in the area that presently isolates them, intergradation could be expected to occur. It stands to reason, however, that *platysayoides* should have subspecific rank, because it is geographically isolated from the main population of *complanata.*

Summary. (1) *Triodopsis complanata* consists of two subspecies: *c. complanata* and *c. platysayoides.* The nominate subspecies combines the former *T. tridentata complanata* and *t. tennesseensis*, whereas *c. platysayoides* corresponds to the former *T. platysayoides.*

(2) The two subspecies of *T. complanata* are geographically isolated from each other. The nominate subspecies geographically replaces *T. tridentata.*

(3) Both subspecies favor low areas. Here they can compete successfully with the related species, *T. tridentata*, which is more successful at higher elevations. The two species as a rule do not invade each other's habitat, thus showing ecological exclusion.

(4) The sculpture seems to vary with the wetness of the habitat to some extent. Other characters show irregular geographic variation.

Triodopsis burchi Hubricht
Plate I: 12–14

Triodopsis tennesseensis subsp. *burchi* Hubricht, 1950, Nautilus 64: 8. From along Route U.S. 58, 3 miles west of Danville, Pittsylvania County, Virginia. Type ANSP 186178.

Definition. Triodopsis burchi corresponds to the former *T. tennesseensis burchi* (*T. tennesseensis* is considered a synonym of *T. c. complanata*).

Description. Shell width 8.9–13.2 mm; height 4.9–6.2 mm, height to width ratio 0.45–0.56; umbilicus 1.5–2.7 mm, umbilicus to width ratio 0.15–0.21; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; subsequent whorls with more pronounced striae, last whorl with 3–4 striae per millimeter; intervals between striae smooth or with granules; umbilical region and shoulder of last whorl always with granules; in some specimens, fine spiral lines (20 per mm) also present near aperture; lines worn off easily, leaving smooth shell; aperture oval-triangular, upper side gently curving, lower almost straight; lip swelling thick to very thick, upper lip swelling bulging near lip tooth; lip teeth moderate to small to almost none; upper to lower tooth ratio 0.78–0.92; parietal lamella moderate to small, corresponding to distal portion of a full parietal lamella, pointing well below upper lip tooth.

Differential diagnosis. Triodopsis burchi "differs from *T. tennesseensis* [*T. c. complanata*] in being much smaller, with a more glossy surface" (Hubricht, 1950b). The two forms are otherwise nearly identical. The glossiness of the shell is due to the almost complete lack of granules on the last whorl; in *c. complanata* this is granulated and hence dull.

Distribution and ecology. Triodopsis burchi is a geographical isolate of *T. c. complanata* (Fig. 3). The Blue Ridge and the Appalachian mountains isolate the two forms. There is a distance of about one hundred miles between the closest *burchi* and *c. complanata* localities. The range of *burchi* is confined to the Inner Piedmont of Virginia, from Pittsylvania County to the Blue Ridge Mountains. The area is covered by mixed oak-pine and oak-chestnut forests. The elevation ranges from 500 to 1500 feet.

The *measured material* comes from the following localities: *Virginia*: Pittsylvania, Henry, and Roanoke counties (ANSP). A total of 3 samples, 2–15 specimens each, 29 specimens altogether.

Variation. As can be expected because of its small population and restricted distribution, the variation of *T. burchi* is limited.

Systematics. Triodopsis burchi was originally ranked by Hubricht as a subspecies of *T. tennesseensis* [*T. c. complanata*]. More recently (1958), he ranked the taxon as a full species, without stating his reasons for the change. It seems to me that either arrangement is acceptable. The only thing that could settle the question, i.e., whether or not the two forms are reproductively isolated, is not known, since they are not in contact in nature. If we assume, as is done here, that the great difference in body size between *burchi* and *c. complanata* could prevent interbreeding, we may assign *burchi* full specific rank. Otherwise we may consider it a subspecies of *T. complanata*.

Summary. Triodopsis burchi is a geographic isolate of *T. c. complanata*, and is presumably reproductively isolated from that species. It is distributed over a small and uniform area. Its variation is limited.

Evolutionary relationships in the complanata-burchi group. Triodopsis c. platysayoides and *T. burchi* are peripheral isolates of *T. c. complanata*, which is an indication that they are relatively recent descendants of the latter form. The fact that *burchi* is much smaller and *c. platysayoides* is larger than *c. complanata* is consistent with this interpretation, since peripheral isolates are the most variable elements of a population (Mayr, 1963). Still another fact supporting the above interpretation is that *c. complanata* has either a smooth or a coarsely striated shell, whereas the two other forms have smooth or finely striated shells. A coarsely striated shell is generally a primitive feature in *Triodopsis* (p. 157).

The *complanata-burchi* group probably evolved from *tridentata*.

THE *RUGOSA* COMPLEX

Definition. The *rugosa* complex contains two taxa, *rugosa* and *fulciden*, which can be considered either distinct species or conspecific subspecies.

Triodopsis rugosa Brooks and MacMillan
Plate I: 15–18

Triodopsis tridentata var. *rugosa* Brooks and MacMillan, 1940, Nautilus 53: 96, pl. 12, fig. 3. Damp ravine, Blair Mountain, 1 mile southwest of Blair, Logan County, West Virginia. Paratype ANSP 174909.

Triodopsis rugosa var. *anteridon* Pilsbry, August 1, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 803, fig. 477. Valley Forge, Carter County, Tennessee. Type ANSP 150304.

Definition. Triodopsis rugosa combines the former *T. r. rugosa* and *r. anteridon.*

Description. Shell width 10.6–15.5 mm; height 5.4–7.2 mm, height to width ratio 0.42–0.54; umbilicus 1.7–3.6 mm, umbilicus to width ratio 0.16–0.23; embryonic whorls

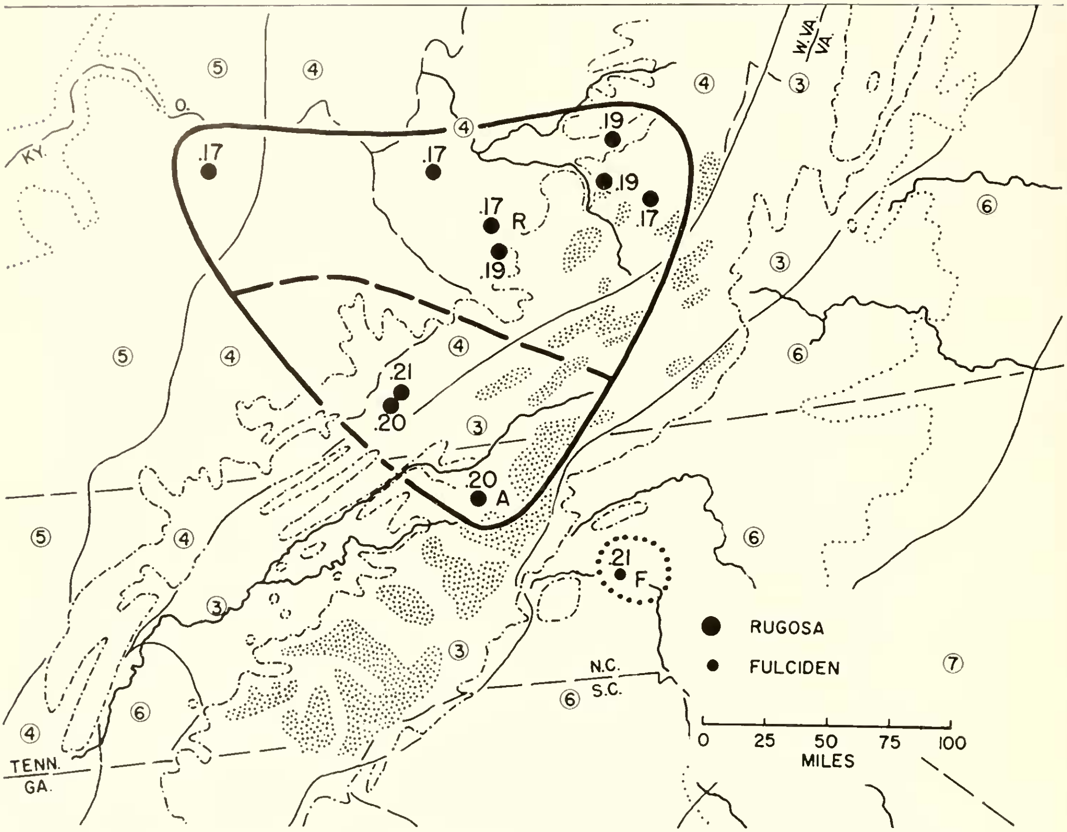


Figure 7. Distribution of *Triodopsis rugosa* and *fulciden*, and the geographic variation of the umbilicus to width ratio in *rugosa*. Thick, solid line surrounds the range of *rugosa*; thick, dashed line separates the samples with a narrow umbilicus (umbilicus to width ratio 0.17–0.19) from those with a somewhat wider umbilicus (0.20–0.21); dotted line surrounds the range of *fulciden*. A, type locality of *anteridon*, considered synonymous with *rugosa*; F, *fulciden*; R, *rugosa*. Numbers without a circle are mean values of samples in umbilicus to width ratio. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

1.4–1.5, with striae below suture; striation becoming more pronounced on subsequent whorls; last whorl with 4–5 striae per millimeter; intervals of striae with fine, oblong granules or delicate spiral lines except on shoulder, which is always granulated; aperture trapezoid, or upper side rounded, lower straight; upper lip swelling thin to very thick, lower lip swelling always thick, forming a straight ledge; upper lip tooth often smaller than lower, somewhat receding, and supported below by a slanting buttress; lower tooth located at or to the left of middle of lower lip; parietal lamella straight, bladelike and outstanding, pointing above upper lip tooth.

Differential diagnosis. Triodopsis rugosa differs from the members of the *tridentata* complex in that the shape of the aperture is a trapezoid (sometimes with a rounded upper side); the upper lip tooth is receding, often smaller than the lower lip tooth, and has a slanted buttress below; the parietal lamella is large and points above the upper lip tooth. In the *tridentata* group, the aperture is oval-triangular, the upper lip tooth is not receding or buttressed, the two lip teeth are equally developed, the parietal lamella is of normal size and points below the upper lip tooth.

Triodopsis rugosa differs from *T. pendula* in that the upper lip tooth is often smaller than the lower lip tooth and is buttressed; the lower lip tooth is near the middle of the lip; the last whorl behind the aperture is less than 1½ times as wide as the penultimate, whereas in *pendula* the upper lip tooth is of normal size or even broader than normal, and not buttressed; the lower lip tooth is to the left of the middle of the lip, and the last whorl behind the aperture is 1½ to 2 times as wide as the penultimate one.

Distribution. Triodopsis rugosa is found in a small area which joins West Virginia, Virginia, Kentucky and Tennessee. The *measured material* comes from the following localities (Fig. 7): *Virginia*: Wise County (ANSP, 2 samples; MCZ, 1 sample). *West Virginia*: Greenbrier, Nicholas, Fayette, Lincoln, and Logan counties (CM); Logan County (ANSP, 1 sample; JV, 1 sample). *Kentucky*: Fleming County (ANSP). *Tennessee*: Carter County (ANSP, 1 sample; JV, 1 sample). A total of 13 samples, 1–8 specimens each, 44 specimens altogether.

Ecology. Triodopsis rugosa occurs in oak-chestnut, mixed mesophytic, and western mesophytic forests (Fig. 7). Most localities are in low mountains, around 1500 feet elevation. Brooks and MacMillan stated (1940) that *rugosa* "is found particularly in ravines and valleys that are narrow and damp." The mountainous character of the range is reflected in the variation of the aperture, as discussed below.

Variation. Aperture: The lip swelling and the parietal lamella vary from thin to very thick. From the observation that several species of *Triodopsis* (*tridentata*, *fraudulenta*, *f. fallax*, *m. mullani*) have a stronger armature at high elevations than at low ones, one can infer that this is the case also in *rugosa*. I do not, however, have information on the exact elevation at which the samples were collected; thus this has not been confirmed. The significance of the strong armature is not known.

Sculpture: The intervals of the striae on the last whorl are covered by papillae, fine spiral lines or, in places, by structures intermediate between papillae and spiral lines. The latter structures can be envisioned as papillae with linear extensions on the two sides. Through these structures, the papillae and spiral lines intergrade. Shells with predominantly papillose sculpture occur in the northern and western parts of the range, those with spiral lines, in the southern and eastern parts (Fig. 8).

Measured characters: The width of the shell is correlated with height and umbilicus, not with aperture or sculpture. All characters show irregular geographic variation, except the umbilicus to width ratio, which increases from north to south (Fig. 7). The discordancy between the variation of the latter character and shell width is evident. Therefore, these characters should not be used as the basis for dividing the species into subspecies. Unfortunately, exactly this was done by Pilsbry (1940).

Systematics. According to Pilsbry (1940), *Triodopsis r. anteridon* (Pl. I, figs. 17, 18) is larger, more finely striated, and has a larger umbilicus than *T. r. rugosa.* It may be added that *anteridon* also has a weak armature and a sculpture of spiral lines, whereas *rugosa* has a strong armature and strong papillae. The distinction breaks down, however, when populations other than the type population are considered. Thus, populations from Lincoln and Logan counties, West Virginia, have strong armature and papillae like *rugosa*, but are as large as *anteridon*; their umbilicus is intermediate between the two. Conversely, another population from Fayette County, West Virginia, has the spiral lines of *anteridon*, the small size of *rugosa*, and an intermediate umbilicus and aperture. The conclusion is that *anteridon* cannot be taxonomically separated from *rugosa*. It is, rather, a synonym of the latter.

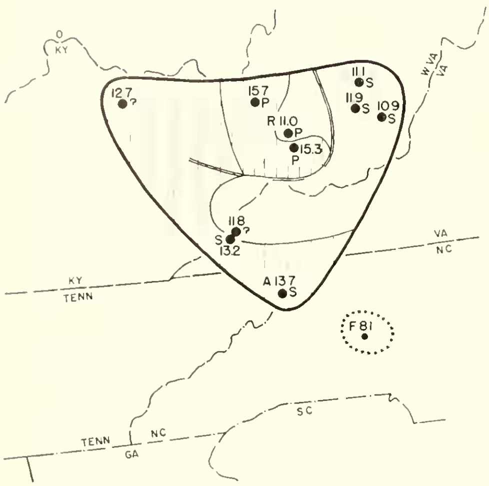


Figure 8. Geographic variation of size (shell width) and sculpture in *Triodopsis rugosa* and *fulciden*. S, spiral sculpture; P, papillate sculpture; ?, sculpture not examined; thin, parallel line separates the samples with papillate sculpture from those with spiral sculpture. Numbers are mean values of samples in size, expressed in millimeters; samples with small size, 10.9–11.0 mm, are separated from the intermediate ones, 12.7–13.7 mm, and the large ones, 15.3–15.7 mm, by a single, thin, solid line. The variation of the two characters is discordant. For other symbols, see Figures 3 and 7.

Summary. *Triodopsis rugosa* is a monotypic species; it includes *T. r. anteridon* as a synonym. It occurs in a relatively small and mountainous area. The aperture probably varies according to the elevation of the habitat; the umbilicus to width ratio varies clinally from north to south; other characters vary irregularly. The variation is thus discordant.

Triodopsis fulciden Hubricht
Plate I: 19–21

Triodopsis fulciden (*sic!*) Hubricht, 1952, Nautilus 65: 81. Upland oak woods, 3.4 miles west of Conover, Catawba County, North Carolina. Holotype ANSP 188292, paratypes ANSP 188290.

Definition. The name *fulciden* is used here as proposed by its author.

Description. Shell width 7.7–8.6 mm; height 4.0–4.3 mm, height to width ratio 0.49–0.53; umbilicus 1.4–1.9 mm, umbilicus to width ratio 0.18–0.23; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striation becoming more pronounced on subsequent whorls; 3–4 striae per millimeter on last whorl; no fine sculpture visible on the studied shells, which were slightly worn; aperture a trapezoid with rounded upper arch; upper and lower lip swelling thick, forming an angle in right lower corner of aperture; upper lip tooth small, having a slanted buttress below, lower lip tooth of normal size; parietal lamella large, straight, outstanding, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis fulciden* differs from *T. rugosa* in its smaller size; otherwise they are very similar. They are comparable to *T. burchi* and *T. complanata* in this respect; these are also extremely similar except for body size.

Hubricht states that "*T. rugosa* . . . has an aperture very similar to *T. tridentata*, whereas the aperture of *T. fulciden* is more suggestive of *T. fraudulenta*" (1952a: 81). To me, the aperture of *fulciden* is not at all similar to that of *fraudulenta*.

Distribution and ecology. *Triodopsis fulciden* is confined to the Catawba River Valley, in Catawba County, North Carolina (Fig. 7). This area lies in the Piedmont region of the Appalachians, between 1000 and 1500 feet elevation. It is covered by mixed oak-pine forests. Only 3 samples, 9 specimens altogether, were available for study from the ANSP and my own collecting.

Triodopsis fulciden is a geographical isolate of the related species *T. rugosa*, which lives west of the Appalachians (Fig. 7). The horizontal distance is only about 65 miles between the two species, but this is enough to isolate them well, since the high ranges of the Appalachians stretch across this area. This distribution shows a conspicuous resemblance to that of *T. complanata* and *T. burchi*, which probably results from similar evolutionary history.

Variation. This is limited, as can be expected from the small population and the restricted range of the species.

Systematics. Triodopsis fulciden is treated here as a taxon specifically separate from *T. rugosa*, on the assumption that the two forms are reproductively isolated because they differ pronouncedly in body size. It is admitted, however, that this assumption cannot be tested, since the two forms are allopatric in distribution. Such cases are manifestations of what Wilson and Brown (1953) call the "uncertainty principle" in taxonomy.

Evolutionary relationships. Triodopsis fulciden is a peripheral isolate of *T. rugosa*, and on this basis it seems certain that it evolved from the latter in relatively recent times, through geographical isolation. The *rugosa* complex is closely related to the *tridentata* complex. It is not known, however, when the two groups became separated.

Summary. Triodopsis fulciden is a geographic isolate of *T. rugosa*. It has probably achieved reproductive isolation from that form. It occupies a small area; its variation is limited.

THE *JUXTIDENS* COMPLEX

Definition. This complex contains a single species, *T. juxtidens*, with three subspecies: *j. juxtidens*, *j. stenomphala*, and *j. discoidea*. There is some question, however, as to whether the last subspecies should properly be included in *T. juxtidens*, or should be considered a separate species.

Triodopsis juxtidens (Pilsbry)
Triodopsis juxtidens juxtidens (Pilsbry)
Plate II: 1–3

Polygyra tridentata var. *juxtidens* Pilsbry, 1894, Proc. Acad. Nat. Sci. Philadelphia 46: 20, pl. 1, fig. 8. Limestone region, Cave Town, Washington County, Maryland. Type ANSP 64720.

Polygyra tridentata juxtigens F. C. Baker, 1898, Trans. St. Louis Acad. Sci. 8: 84. Pinnacle Hill, southeast Rochester, Monroe County, New York.

Definition. Triodopsis j. juxtidens corresponds to a portion of the former *T. tridentata juxtidens*. The other portion is *T. j. stenomphala*, described in the present paper as a new subspecies (p. 169). *Triodopsis j. juxtidens* contains those populations of the species which have mean values of 60–90, occasionally 55, in character index. The method of computing character index is shown in Table II.

Description. Shell width 11.0–19.1 mm; height 5.3–9.9 mm, height to width ratio 0.46–0.61; umbilicus 1.7–3.5 mm, umbilicus to width ratio 0.12–0.19; number of whorls 4.7–6.0, whorl to width ratio 0.29–0.46; embryonic whorls 1.4–1.5, finely striated below suture, smooth elsewhere; subsequent whorls with regular and more pronounced striation, 3.4 striae per millimeter on last whorl; intervals between striae with sparse granulation, except in umbilical region where granulation is dense; aperture square to circular; lip swelling and lip tooth nearly marginal to slightly receding; when circular aperture combines with receding lip swelling and lip teeth, aperture is called dish-like; upper lip tooth is slightly receding, usually broadened, sometimes bifid; lower lip tooth marginal; upper and lower lip teeth in close proximity (hence the name "*juxtidens*"); parietal lamella arcuate to straight, pointing above upper lip tooth, its proximal portion often low, like a callus.

Differential diagnosis. Triodopsis j. juxtidens differs from *T. tridentata* in that the upper and lower lip teeth are close together, and therefore the distance between them is smaller than the distance between the upper lip tooth and the juncture of the upper lip with the shell (Fig. 6); also, the upper lip tooth is usually broadened and slightly receding, with the parietal lamella pointing above it. In *T. tridentata* the lip teeth are farther apart, the upper lip tooth is very rarely broadened or receding, and the parietal lamella points at or below the upper lip tooth. *Triodopsis n. vulgata*, another similar form, has a wider umbilicus and a more capacious last whorl than *T. j. juxtidens*, and an upper lip tooth that is much broader and deeply receding.

Distribution. Triodopsis j. juxtidens

Table II

Chart for Computing Character Index in *Triodopsis juxtidens*. Method of Calculation: a Specimen Having a Width of 18.0 mm, an Umbilicus to Width Ratio of 0.18, a Whorl to Width Ratio of 0.30, a Parietal Lamella to Width Ratio of 0.17, and an Aperture of "*juxtidens*" Was Scored 30 + 15 + 15 + 20 + 20 = 100, the Available Maximum Score.

Score	Width in mm	Umbilicus to width ratio	Whorl to width ratio	Parietal lamella to width ratio	Aperture	
0	9.8–10.9	0.9–0.10	0.46–0.51	0.30–0.32	*stenomphala*	*j. stenomphala*
5	11.0–12.1	0.11–0.13	0.40–0.45	0.26–0.29		↑
10	12.2–13.3	0.14–0.16	0.34–0.39	0.22–0.25	intermediate	❘
15	13.4–14.6	0.17–0.19	0.29–0.33	0.18–0.21		❘
20	14.7–15.9			0.15–0.17	*juxtidens*	❘
25	16.0–17.1					↓
30	17.2–18.3					*j. juxtidens*

ranges along the eastern seaboard from Vermont to Georgia and westward to West Virginia (Fig. 9). It slightly overlaps *T. tridentata*, as discussed below.

A record from Davenport, Scott County, Iowa (MCZ 47473, ex J. D. King) appears to be incorrect, since this locality lies very far outside the normal range. I also regard the records from Isle au Haut, Knox County, Maine (MCZ 14685, 14686 and 14687) as suspect, because the record is outside the normal range, and the habitats on the island (coniferous forests) seem unsuitable for the snail. Three days were spent in an attempt to verify this record, but without success.

The occurrence of *T. j. juxtidens* in West Virginia was first reported by MacMillan (1950). Since Pilsbry in his comprehensive work (1940: 799) explicitly stated that "It [*j. juxtidens*] is not known to occur west of the mountains," verification of the West Virginia records seemed desirable. Half of MacMillan's *j. juxtidens* material indeed proved to be misidentified *T. tridentata* or *T. rugosa*, but the other half was "good" *j. juxtidens*. The occurrence of the subspecies on the western side of the Appalachians thus can no longer be doubted.

This extension of the range of *j. juxtidens* to the western side of the Appalachians probably took place in recent times. We can infer this from two facts. First, only a single valley system has been colonized. The MacMillan collection covers all of West Virginia, and contains enough material to state this with confidence. Secondly, the colonizing population as a whole has not yet become morphologically different (except for one single deme that is intermediate between *j. juxtidens* and the western subspecies, *j. discoidea* [p. 173]). If this inference is true, the snail must have moved at least 90 miles down the valley in a few thousand years, a relatively "fast" dispersal rate for the slow-moving snails. It is probable that this was accomplished, in part at least, by rafting or being washed down the Kanawha River. Similar inferences can be drawn from the distribution of *T. fraudulenta* and *T. m. mullani*.

At present the colonizing populations have approached to within 110 miles of the eastern range limits of *j. discoidea*, the most westerly occurring subspecies. It will be interesting to observe what happens when the two forms establish actual contact.

T. j. juxtidens crossed the mountains through the upper valleys of the Kanawha and Roanoke river systems (Fig. 9). The effectiveness of valleys as dispersal routes is emphasized by the fact that several other cases are known in *Triodopsis* in which the snails have used similar paths of dispersal. Thus a stock of *T. c. complanata* reached the eastern side of the Appalachian Mountains via the Holston and Roanoke val-

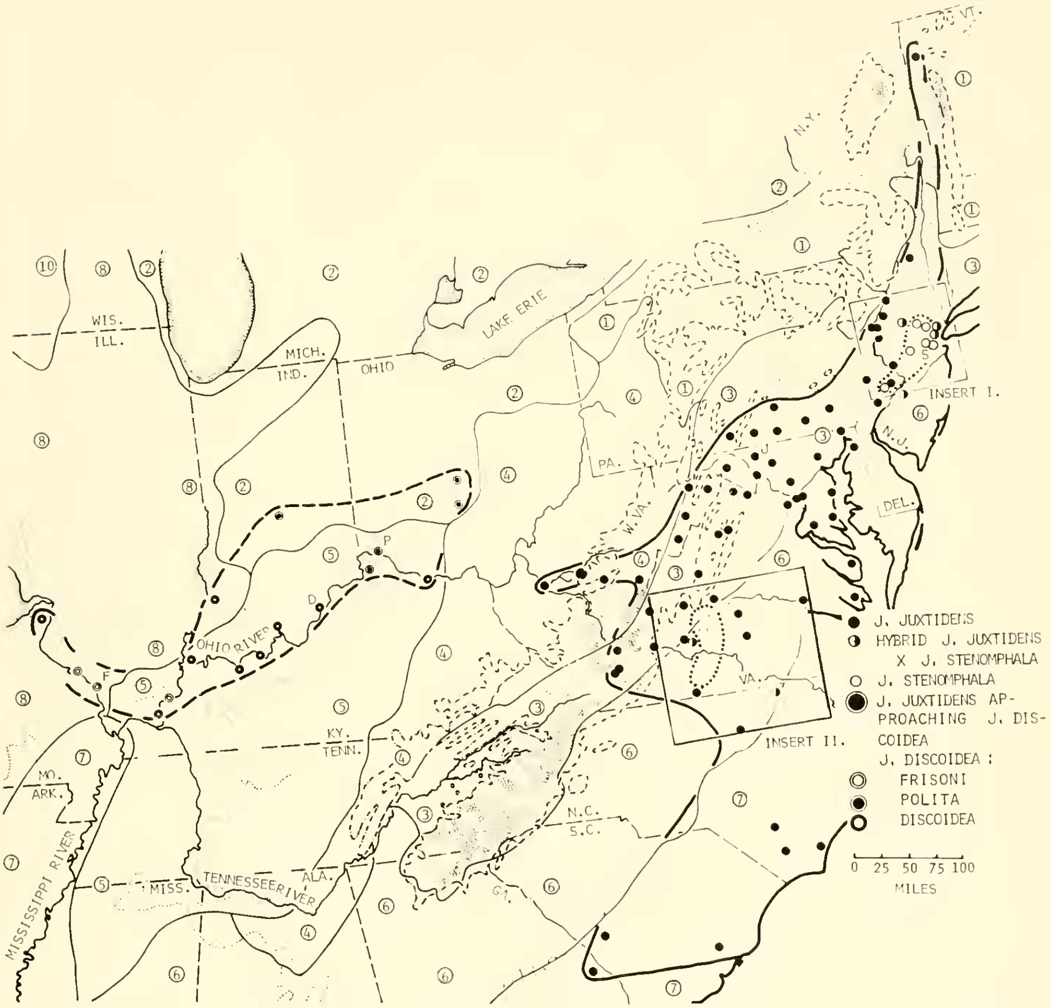


Figure 9. Distribution of *Triodopsis juxtidens*. Thick solid line surrounds the range of *j. juxtidens*; thick, dashed line, *j. discoidea*; dotted line, *j. stenomphala*. D, type locality of *j. discoidea*; F, *frisoni*; J, *j. juxtidens*; P, *polita*; S, *j. stenomphala*. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3. The two inserts are shown in Figure 10.

leys, and one of *T. rugosa*, via the Holston and French Broad, and Yadkin and Catawba valleys (Figs. 3, 7). Speaking in phytogeographic terms, the valleys are "straits" of deciduous forests between "islands" of coniferous forests that cover the peak regions (Fig. 19). The straits are evidently favorable for the passing of snails adapted to the deciduous forests.

The *measured material* comes from the following localities: *Vermont*: Chittenden County (MCZ). *Pennsylvania*: Pike and Lancaster counties (MCZ); Monroe, Northampton, Bucks, and Philadelphia counties (ANSP). *New Jersey*: Sussex and Warren counties (MCZ). *Maryland*: Washington and Baltimore counties (ANSP); Charles County (MCZ). *West Virginia*: Jefferson County (ANSP); Nicholas and Kanawha counties (CM). *Virginia*: Shen-

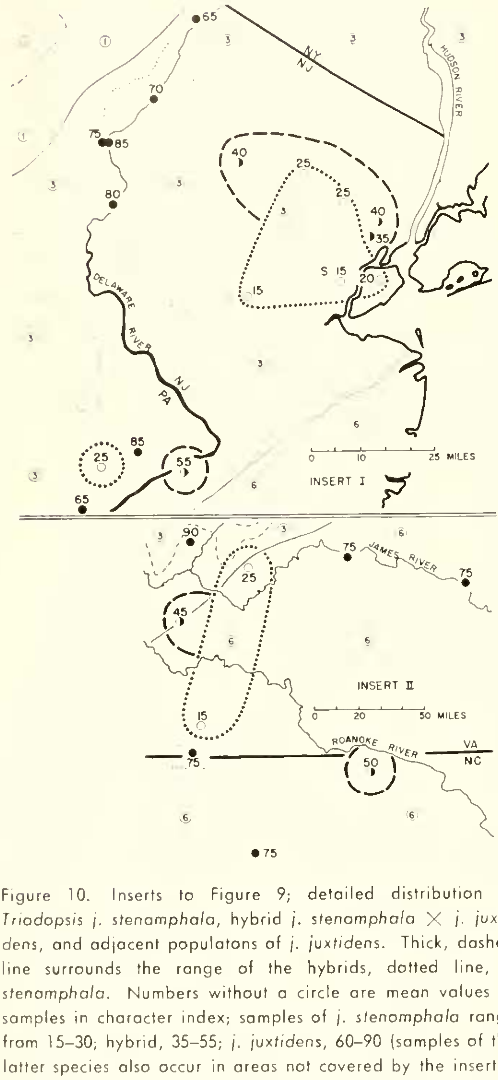


Figure 10. Inserts to Figure 9; detailed distribution of *Triodopsis j. stenomphala*, hybrid *j. stenomphala* × *j. juxtidens*, and adjacent populatons of *j. juxtidens*. Thick, dashed line surrounds the range of the hybrids, dotted line, *j. stenomphala*. Numbers without a circle are mean values of samples in character index; samples of *j. stenomphala* range from 15–30; hybrid, 35–55; *j. juxtidens*, 60–90 (samples of the latter species also occur in areas not covered by the inserts). Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3, except that the state lines are marked with thick, solid lines.

andoah, Rockbridge, Warwick, and Pittsylvania counties (ANSP); Fairfax, Northumberland, Buckingham, and Henrico counties (MCZ). *Washington, D.C.*: Zoological Park (MCZ). *North Carolina*: Durham, Bladen, and New Hanover counties (ANSP); Columbus County (MCZ). *South Carolina*: Aiken and Orangeburg counties (ANSP). A total of 30 samples, 1–32 specimens each, 248 specimens altogether.

Ecology. Triodopsis j. juxtidens occurs in northern hardwoods, mixed mesophytic, oak-chestnut, oak-pine and southeastern evergreen forests, between sea level and 2000 feet (Fig. 9). It is often found on riverbanks (Hubricht, 1950b; own experience).

Triodopsis j. juxtidens slightly overlaps the related species *T. tridentata*. Pilsbry states (1940: 799) that in the zone of overlap "in any suitable place either *tridentata* or *juxtidens* is to be found, but never the two together, in my experience; however, A. F. Archer reports finding them together at Lambertville, New Jersey." My experiences in New Jersey and Pennsylvania seem to verify Pilsbry's observations. The two species probably have very similar ecological requirements; therefore they cannot coexist in the same habitat for a long period of time. This is another example of ecological exclusion.

Triodopsis j. juxtidens probably shows habitat exclusion with *T. f. fallax* and *f. obsoleta*, also. More collecting should be done, however, to more firmly establish this observation.

Variation. The various elements of the *aperture*, such as the lip swelling, lip teeth, parietal lamella and outline of the whole aperture, vary irregularly through the greater part of the range of the species. Some regularity can be observed, however. Thus, at the southern end of the range, most specimens have an aperture almost circular in outline, evenly and deeply receding lip swelling and lip teeth (dish-like aperture), and a long parietal lamella. In marshy areas most specimens have a normal aperture with a nearly straight parietal lamella. Neither of these groups qualifies as a subspecies; the first group occurs in too limited an area and is too weakly characterized, the second group is primarily an ecological form.

Of the *measured characters*, width of shell is correlated with height, umbilicus and whorl number. All measured characters show irregular geographic variation.

The variation of the character index is discussed in a later section.

Systematics. Triodopsis j. juxtidens was formerly considered a subspecies of *T. tridentata.* It should be considered, however, distinct from it. It maintains its identity even in areas where it overlaps *tridentata*, demonstrating its reproductive isolation from that form. Previous authors who combined them in one species overlooked this.

Triodopsis juxtidens stenomphala subsp. n. Plate II: 7–9

Holotype: MCZ 18159a. Acquired from the Bland Collection, collector and date of collecting not known. *Paratypes*: MCZ 18159b; other data as above. The name *stenomphala*, meaning "of narrow umbilicus," expresses an outstanding feature of the new form.

Type locality: Rahway, Union County, New Jersey.

Definition. Triodopsis j. stenomphala contains those populations of the species having mean values of 15–30 in character index. (The method of computing character index is shown in Table II.)

Description. Shell width 9.8–13.5 mm; height 5.6–7.8 mm, height to width ratio 0.50–0.59; umbilicus 1.1–1.8 mm, umbilicus to width ratio 0.39–0.49; embryonic whorls and sculpture as in *j. juxtidens*, except for a reduction in number of granules; aperture square; lip swelling well developed and nearly marginal, so that edge of peristome is slightly swollen; lip teeth moderately large, upper lip tooth slightly receding, lower lip tooth marginal; parietal lamella large, long, and nearly straight, pointing above upper lip tooth.

Differential diagnosis. Triodopsis j. stenomphala differs from *j. juxtidens* in having a narrower umbilicus, a tighter coiling of the whorls, and a larger and longer parietal lamella. Other, less important diagnostic features are the smaller dimensions of the shell and the squarish, swollen aperture. The marsh-dwelling populations of *j. juxtidens* may be very hard to separate from *j. stenomphala*, since they are also small and have long, straight parietal lamellae.

Distribution. Triodopsis j. stenomphala has a disjunct distribution. It occurs in three small areas in New Jersey, Pennsylvania, and Virginia (Figs. 9, 10), the first two of these possibly being connected. In New Jersey and probably in Pennsylvania it is allopatric with *j. juxtidens*; in Virginia, it is "sympatric," although not coexistent. According to Hubricht, the two forms occupy different habitats in Virginia (see below).

The Virginian occurrence is possibly of recent origin. Perhaps lumber trucks are responsible, as suggested by R. T. Abbott (personal communication, 1962). There is no great need, however, to involve human agencies. The snail could have gotten to Virginia by natural means such as "walking," by being carried by rivers, winds or birds; also, it could be a relict of earlier times, like *T. pendula.* Still another possibility is to assume that the New Jersey—Pennsylvania population evolved independently of the Virginia population; in other words, to assume that *j. stenomphala* is a polytopic subspecies. This seems to me unlikely, however, since the two populations live in different habitats, whereas the populations of a polytopic subspecies are supposed to occur in "identical" habitats. The best explanation would appear to involve natural dispersal and recent origin. At any rate, the Virginia population presently forms a geographic isolate of the New Jersey-Pennsylvania population.

The *measured material* comes from the following localities: *New Jersey*: Morris County (ANSP); Essex, Union, and Somerset counties (MCZ). *New York*: Richmond County (MCZ). *Virginia*: Amherst and Pittsylvania counties (ANSP). A total of 8 samples, 2–8 specimens each, 34 specimens altogether.

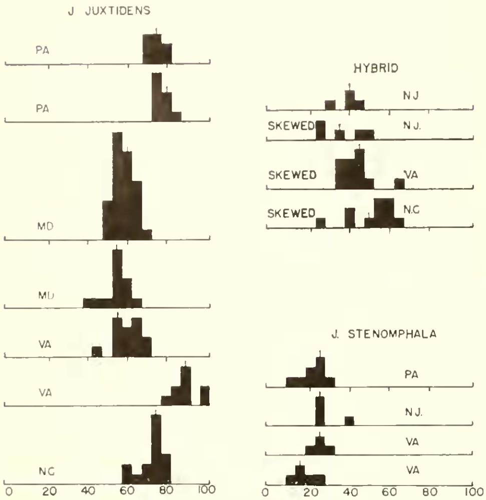


Figure 11. Character index histograms of samples of *Triodopsis j. juxtidens, j. stenomphala*, and hybrids between the two subspecies. Short line on top of column indicates mean value of sample. The histograms of most hybrid samples are strongly skewed, those of the parental forms slightly skewed or normal. The abbreviations stand for the states where the samples have been collected. Scale in character index units.

Ecology. In the New Jersey-Pennsylvania area, *T. j. stenomphala* is found on both low and high ground. In Virginia, however, it ". . . is common in upland oak woods in the Outer Piedmont," whereas on the river bluffs another form, *j. juxtidens*, is abundant (Hubricht, 1950b). Thus it seems that in the New Jersey-Pennsylvania area the subspecies occupies a wider range of habitats than in Virginia. In view of the fact that in the former area no related form occurs, whereas in the latter area *j. juxtidens* is present, we may assume that the restriction to the uplands is caused by the presence of, or more specifically, the competition provided by, the related form, which is superior on the river bluffs. The situation is very complex, however. *Triodopsis j. stenomphala* and *j. juxtidens* not only seem to compete but also to hybridize with each other. This, of course, cannot go on indefinitely. If hybridization continues, the two forms will merge. If the hybrids are of reduced viability, hybridization will cease, and each group will be restricted to a single kind of habitat, either upland or lowland.

A similar situation can be observed in *T. complanata.* There, too, one subspecies has a broader and the other a narrower ecological range, and the latter is "sympatric" with the related form, *T. tridentata.* Interestingly, in both cases, the subspecies with the smaller population size has the evolutionarily more advanced, narrower (more specialized) range. This may be because a population of small size may reorganize its genetic constitution more rapidly than a population of large size (Mayr, 1954; 1963: 527); such reorganization is probably necessary for changing the ecological range.

Systematics. Triodopsis j. stenomphala is sufficiently distinct to be recognized as a taxonomic unit. This was shown in the description and differential diagnosis. It cannot be considered a full species, however, because it freely interbreeds with *j. juxtidens.* The evidence for this is discussed below.

Hybrid populations between *Triodopsis j. juxtidens* and *j. stenomphala*

Plate II: 4–6

Some populations of *Triodopsis juxtidens* are intermediate between the two subspecies according to their character index; they have mean values of 35–55, as compared to 15–30 for *j. stenomphala* and 60–90 for *j. juxtidens.* These populations are considered to be of hybrid origin for the following reasons. First, they show a greater variation than the "pure" populations of either *j. juxtidens* or *j. stenomphala*, as demonstrated by comparison of their character index histograms (Fig. 11), or of the range of variation (Fig. 4). Second, these populations are found in the zone of contact between the two subspecies (Figs. 9 10).

Attention should be called to the fact that the character index histograms of most hybrid populations are skewed (Fig. 11).

The same phenomenon, though even more pronounced, can be observed in the hybrids of *T. f. alabamensis* with *f. fallax* and *f. obsoleta* (Fig. 18). A skewed distribution curve is not a necessary criterion of hybrid origin, and it may only be accidental that in *Triodopsis* so many hybrid populations have this attribute. The phenomenon is best explained by the introduction of one or a few specimens of parent A into a population of parent B with subsequent maintenance of the resulting imbalance.

Hybrid samples have been *measured* from the following localities: *New Jersey*: Burlington, Hudson, and Essex counties (MCZ); Morris County (ANSP). *Virginia*: Bedford County (MCZ). *North Carolina*: Warren County (ANSP). A total of 6 samples, 1–12 specimens each, 35 specimens altogether.

In New Jersey, the hybrid populations live both in the hills and on the riverbanks, just as the parent populations do. I do not have enough information on the habitat of the hybrids living in the Virginia area.

The occurrence of hybrid populations is important taxonomically, because it proves the conspecificity of what are called here *j. juxtidens* and *j. stenomphala*.

Triodopsis juxtidens discoidea (Pilsbry) Plate II: 10–11

Polygyra tridentata subsp. *discoidea* Pilsbry, 1904, Nautilus 17: 142. Charlestown Landing, Clark County, Indiana. Type ANSP 11076.

H(elix) tridentata subsp. *polita* Wetherby, 1894, Nautilus 8: 44. Limestone cliffs above Cincinnati, Hamilton County, Ohio. Not *Helix polita* Pulteney, 1797, or Mueller, 1774. Type ANSP 98940.

Polygyra tridentata var. *frisoni* F. C. Baker, 1933, Nautilus 47: 58. South end of Fountain Bluff, Jackson County, Illinois. Paratypes ANSP 161146.

Definition. Triodopsis j. discoidea corresponds to *T. tridentata discoidea* of Pilsbry (1940). A character index was not prepared for this taxon.

Description. Shell width 12.9–20.9 mm; height 5.8–10.0 mm, height to width ratio 0.40–0.54; umbilicus 2.2–4.6 mm, umbilicus to width ratio 0.14–0.23; embryonic whorls 1.4–1.5, faintly or definitely striated below suture, smooth otherwise; striation becoming more pronounced on subsequent whorls, 3–5 striae per millimeter on last whorl; striae from very low to moderately high, their intervals almost smooth, or with fine or pronounced granules; aperture trapezoid to oval-triangular; lip swelling and lip teeth well developed, somewhat receding; upper lip tooth usually broad and flat; upper and lower teeth close to each other; parietal lamella moderately developed, arcuate, pointing slightly above upper lip tooth.

Differential diagnosis. Triodopsis j. discoidea differs from *j. juxtidens* by its larger and flatter shell, which is often smooth and shiny, flatter aperture, and wider umbilicus. From *T. tridentata* it differs in various apertural features; the lip teeth are in close proximity, the distance between them being much less than the distance that separates the upper lip tooth from the junction of the upper lip with the shell; the upper lip tooth is broad and slightly receding, with the parietal lamella pointing above it; the shell is flat and the umbilicus is wide. In contrast, the lip teeth of *tridentata* are farther from each other, the upper lip tooth is not broad or receding, the parietal lamella points at or below it, the shell is higher and the umbilicus narrower.

Distribution. Triodopsis j. discoidea occurs in the Ohio and the Mississippi valleys (Fig. 9). Its range is partially separated from that of its closest ally, *j. juxtidens*, by the Appalachian Mountains. The separation was once more complete, but has broken down in the Kanawha River valley in recent times (p. 166).

The *measured material* comes from the following localities: *Ohio*: Franklin, Brown, and Hamilton counties (2 samples, both

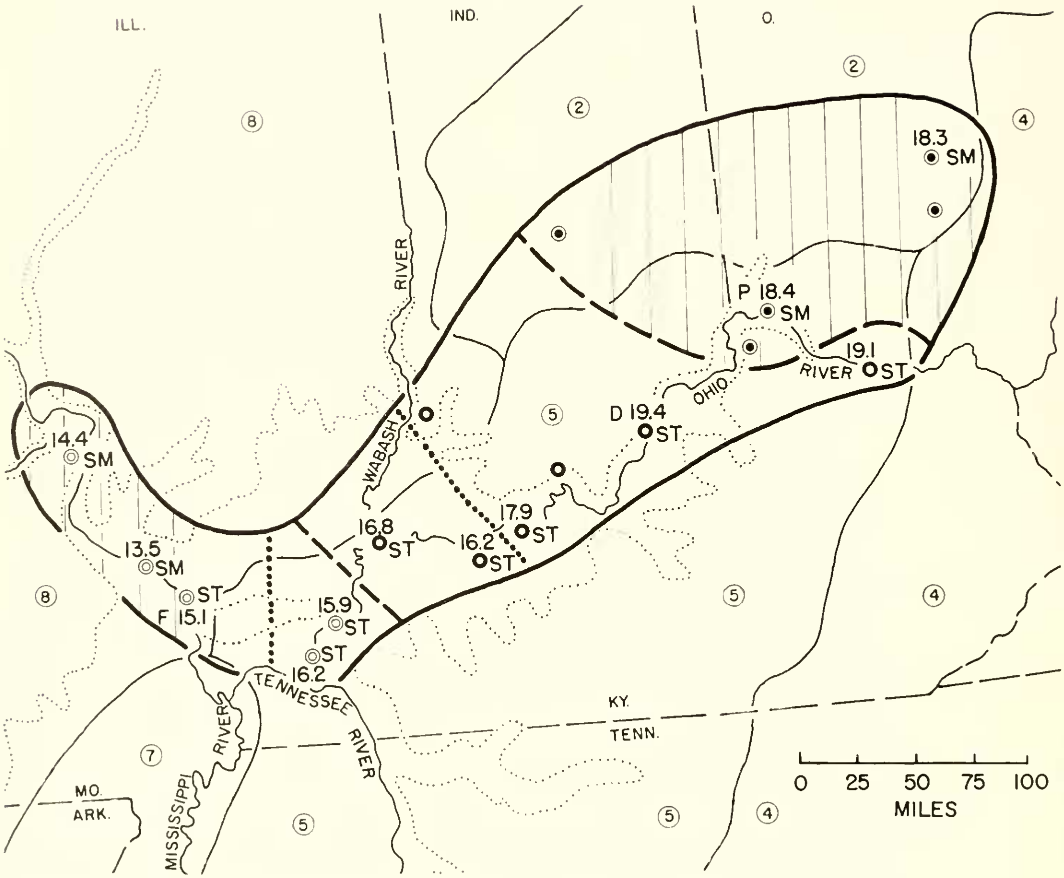


Figure 12. Geographic variation of size (shell width) and sculpture in *Triodopsis j. discaidea*. Thick, solid line surrounds the range of the subspecies; thick, dashed line separates *polita*, *discoidea*, and *frisoni*, all included in *j. discaidea*; dotted line separates the samples with small size, 13.5–15.1 mm, from intermediate, 15.9–16.8, and large, 17.9–19.4. The size shows a gradual increase from the west to the east; the sculpture does not. Thus, the two characters vary discordantly. SM, smooth sculpture; ST, striated sculpture. Other symbols as in Figure 9.

ANSP). *Indiana*: Perry, Posey, and Clark counties (ANSP). *Illinois*: Randolph, Jackson, Pope, and Hardin counties (ANSP). *Kentucky*: Davies County (MCZ). *Missouri*: St. Louis County (ANSP). A total of 13 samples, 3–15 specimens each, 94 specimens altogether.

Ecology. Triodopsis j. discoidea is largely confined to the valleys of two major rivers, the Mississippi and the Ohio. It seems to prefer the immediate vicinity of the rivers, according to various collectors who have found it on river banks or on cliffs near the rivers. The area is covered by beech-maple, oak-hickory and western mesophytic forests. It lies between 300 and 500 feet (Fig. 9).

Pilsbry (1940: 800) quotes Daniels as saying that in Indiana *T. j. discoidea* "occurs on the immediate banks of the Ohio River, but when you go back into the country you get the typical *tridentata*." If so, this is another example of habitat exclusion. We can assume that *j. discoidea* and *tridentata* once had broader and overlapping ecological spectra, and therefore were competing with each other. In time, however, *j. discoidea* became adapted to the more humid habitats, while the *tridentata* populations of the area became adapted to the drier habitats. This resulted in the habitat exclusion that can be observed at present. The advantage of this arrangement is that it reduces direct competition between the two forms. A similar arrangement exists between *T. c. platysayoides* and *T. tridentata*, and between *j. juxtidens* and *j. stenomphala*.

Plant associations apparently play no direct role in determining the distribution of the subspecies. This is evidenced by the lack of correlation between the subspecies border and the boundaries of the plant associations in the area (Fig. 9).

Variation. The *sculpture* varies from smooth to striated. The former condition is usually associated with moist habitats, as in the case of *c. complanata.* It is not definitely known whether this character has a genetic basis or is a purely environmental modification, but as not all shells from moist habitats are smooth, the former assumption is apparently correct.

Measured characters: Shell width is correlated with height and umbilicus. The shell width increases clinally from west to east (Fig. 12), one of the few instances of this phenomenon in *Triodopsis.* The height to width, and umbilicus to width ratios show irregular geographic variation.

It should be pointed out that sculpture and shell width vary discordantly. The sculpture changes from smooth to striated and back to smooth from east to west, whereas the width grades from small to large in the same geographic sequence. It follows that neither these characters nor their combinations can serve as key taxonomic characters, although they have been used as such in the past.

Systematics. Triodopsis j. discoidea was formerly considered a subspecies of *T. tridentata.* In fact, however, it is specifically separate from that form, since it is reproductively and ecologically isolated from it. Reproductive isolation may be inferred from the discontinuity between the two forms in certain morphological features, which exists in spite of their "sympatric" distribution. These features were listed previously. It is clear that were *j. discoidea* and *tridentata* conspecific, such discontinuities would not exist. The occurrence of ecological isolation was discussed in the section above.

The very same characters that separate *discoidea* from *tridentata* connect *discoidea* with *juxtidens* (see Plates I and II, and the descriptions of the two forms). The only question is whether *discoidea* should be ranked as a subspecies of *juxtidens* or whether it should be treated as a separate species. On the assumption that they would interbreed should they come in contact, we will consider them conspecific. This assumption is justified, since intergrading populations between the two forms occur. On the above basis, the name *T. tridentata discoidea* should be changed to *T. juxtidens discoidea.*

Under the name *discoidea*, Pilsbry combined three taxa: *discoidea*, *polita*, and *frisoni* (1940: 800). I agree with this action. It is true that the three forms differ slightly in sculpture and size, *polita* being large and smooth, *discoidea* medium to large and striated, and *frisoni* medium to small and smooth or striated. But the variation in size and sculpture is gradual and discordant, so that a classification based upon size and sculpture variations would not be valid.

Triodopsis j. juxtidens population approaching *j. discoidea*

A population of *j. juxtidens*, collected in the valley of the Kanawha River, Clay County, West Virginia (CM: 5 specimens), consists of shells which are larger and flatter, and which have a flatter aperture than do those of normal *j. juxtidens.* They clearly approach *j. discoidea* in these characters. They are not smooth, however, as *j. discoidea* usually are, but striated and

TABLE III

MEASUREMENTS OF THE CLAY COUNTY *J. JUXTIDENS* POPULATION. FOR COMPARISON, THE MEASUREMENTS OF REPRESENTATIVE *J. JUXTIDENS* AND *J. DISCOIDEA* POPULATIONS ARE ALSO SHOWN. THE CLAY COUNTY POPULATION APPARENTLY OCCUPIES AN INTERMEDIATE POSITION BETWEEN *J. JUXTIDENS* AND *J. DISCOIDEA*.

Name	Remark	Locality	Number of Specimens	Mean of Width in mm	Mean of Height to Width Ratio	Mean of Umbilicus to Width Ratio	Sculpture
j. juxtidens		West Virginia, near the Clay County population	1	15.5	0.52	0.16	striated
j. juxtidens	second largest in subspecies	Virginia	9	17.1	0.51	0.16	striated
j. juxtidens	widest umbilicus in subspecies	West Virginia	2	14.8	0.52	0.18	striated
j. juxtidens approaching *j. discoidea*		Clay County, West Virginia	5	18.5	0.49	0.17	striated
j. discoidea	easternmost *j. discoidea*	Ohio	5	19.1	0.47	0.18	striated
j. discoidea		Ohio	3	18.3	0.49	0.19	smooth
j. discoidea	largest with widest umbilicus in subspecies	Indiana	6	19.4	0.43	0.21	striated

have a narrow umbilicus, as in *j. juxtidens* (Table III). These specimens are apparently intergrading between *j. juxtidens* and *j. discoidea*; I call them *j. juxtidens* only because they are found within the range of this subspecies, and the range of *j. discoidea* starts 110 miles farther west (Fig. 9).[1]

As far as the origin of this population is concerned, there are two possibilities. It might have arisen through interbreeding of the two subspecies, or it might have developed from the local *j. juxtidens* population, under local selection pressure. Since only one small population is involved, statistical methods were not employed to select the right answer. Judging from simple inspection of the material, though, the range of variation seems normal, which supports the second interpretation.

Whichever interpretation is true, the occurrence of an intergrading population indicates the conspecificity of *j. juxtidens* and *j. discoidea*. The first interpretation would indicate that interbreeding actually took place. The second would indicate a great similarity between the two gene pools, and thus the possibility of interbreeding should the two forms come in contact.

Evolutionary relationships. Among the three members of the *juxtidens* complex, *j. juxtidens* approaches the hypothetical ancestor of *Triodopsis* most closely, inasmuch as it has a striated shell and an unspecialized, broad ecological spectrum. That *j. discoidea* is evolutionarily more advanced than *j. juxtidens* is indicated by its smooth shell and specialization for a particular habitat (p. 172). *Triodopsis j. stenomphala* does not have these traits. It is considered a descendant of *j. juxtidens* because it appears to be a geographical isolate

[1] In the spring of 1967 the author and Mr. Paul Blachman collected populations apparently intermediate between *Triodopsis j. juxtidens* and *j. discoidea* at several other localities as well (Bladen, Gallia Co., Athalia and Coal Grove, Lawrence Co., Ohio; Ghent, Carroll Co., Ky.; on the banks of the Ohio River). Furthermore, they found that these populations do not interbreed with *T. j. juxtidens* at all, whereas they interbreed freely with *T. tridentata*. Thus the morphological resemblance of these populations to *T. j. juxtidens* and *T. j. discoidea* has proved to be deceptive.

of that form. It probably developed from a New Jersey *juxtidens* population which was separated from the main population by the Delaware River valley.

The *juxtidens* complex occupies a morphologically intermediate position between the *tridentata* and *fraudulenta* complexes. But nothing is known as to when and under what circumstances the three taxa separated.

Summary. (1) *Triodopsis juxtidens* consists of three subspecies, *j. juxtidens*, *j. stenomphala*, and *j. discoidea*, and of hybrids and intermediates connecting them. The typical subspecies was formerly considered a subspecies of *T. tridentata*; *j. stenomphala* is a new form, formerly included in *j. juxtidens*; *j. discoidea* is the former *T. tridentata discoidea*, including the former *t. polita* and *t. frisoni* as synonyms.

(2) The range of *j. stenomphala* is separated from that of *j. juxtidens* by a hybrid belt. A few populations of *j. stenomphala* "overlap" *j. juxtidens*, also with hybridization. *Triodopsis j. discoidea* is entirely allopatric with *j. juxtidens*. One of the westernmost populations of *j. juxtidens* morphologically approaches *j. discoidea*.

(3) *Triodopsis j. juxtidens* and *j. stenomphala* occupy all available habitats when they are allopatric, but in areas of "sympatric" occurrence, *j. juxtidens* is confined to river banks and *j. stenomphala* to the uplands. Thus the two forms do not coexist, and thereby demonstrate the exclusion principle. *Triodopsis j. discoidea* occurs only in large river valleys, mainly on the river banks. Both *j. juxtidens* and *j. discoidea* show exclusion with *T. tridentata*, and the former also with *T. f. fallax* and *f. obsoleta*.

(4) The geographic variation is generally irregular in all three subspecies. Exceptions are the clinal variation of the shell width (size) in *j. discoidea* and possibly that of the parietal lamella in *j. juxtidens* and the sculpture in *j. discoidea*, which may be correlated with wetness of the habitat.

(5) The combination of *juxtidens*, *stenomphala* and *discoidea* in one species is justified by the fact that hybrids or intergrades occur between them. The taxon thus formed is specifically distinct from *tridentata*, as the two appear to be reproductively isolated.

The *fraudulenta* Complex

Definition. This complex contains four taxa: *Triodopsis fraudulenta*, *T. pendula*, and two subspecies of *T. neglecta*—*n. vulgata* and *n. neglecta*. *Triodopsis fraudulenta* is definitely a distinct species, *T. pendula* is probably so; *T. n. vulgata* and *n. neglecta* are probably conspecific. The central stock from which the other three taxa are derived is *n. vulgata*; therefore the discussion will begin with this taxon.

Triodopsis neglecta (Pilsbry)
Triodopsis neglecta vulgata (Pilsbry)
Plate II: 12–14

Triodopsis fraudulenta subsp. *vulgata* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 805, fig. 478b,c. Columbus, Franklin County, Ohio. Type ANSP 57148.

Triodopsis hopetonensis subsp. *claibornensis* Lutz, 1950, Nautilus 63: 121, fig. 1. Foothills of the Cumberland Mountains near the Grace Nettleton Home for Girls, Harrogate, Claiborne County, Tennessee. Paratype ANSP 215860.

Definition. *Triodopsis n. vulgata* combines the former *T. fraudulenta vulgata* and *T. hopetonensis claibornensis*. It contains those populations of the *fraudulenta* complex which have mean values of 50–75 in character index (Table IV).

Description. Shell width 12.2–19.8 mm, height 5.8–10.6 mm, height to width ratio 0.41–0.63; umbilicus 2.4–5.1 mm, umbilicus to width ratio 0.16–0.30; number of whorls 5.0–6.4, whorl to width ratio 0.30–0.45; upper tooth to lower tooth ratio 1.00–1.29; embryonic whorls 1.3–1.4, finely striated below suture; striation on later whorls becoming more pronounced, 3–4 striae per millimeter on last whorl; space between striae with papillae or fine spiral lines,

TABLE IV

CHART FOR COMPUTING CHARACTER INDEX OF *TRIODOPSIS N. VULGATA*, *N. NEGLECTA*, AND *T. PENDULA*. METHOD OF CALCULATION: A SHELL WITH A WIDTH OF 19.3 MM, A HEIGHT OF 10.5 MM, AN UPPER TOOTH TO LOWER TOOTH RATIO OF 0.99, A WHORL TO WIDTH RATIO OF 0.30, AND AN UMBILICUS TO WIDTH RATIO OF 0.15 WAS SCORED (70 + 65 + 65 + 50 + 50)/3 = 100, MAXIMUM AVAILABLE SCORE.

Score	Width	Height	Upper to lower tooth ratio	Whorl to width ratio	Umbilicus to width ratio	
0	9.9–10.5	3.5–4.0	1.39–1.42	0.50–0.51	0.29–0.30	*n. neglecta*
5	10.6–11.2	4.1–4.5	1.35–1.38	0.48–0.49	0.27–0.28	↑
10	11.3–11.9	4.6–5.0	1.32–1.34	0.46–0.47	0.26	
15	12.0–12.6	5.1–5.5	1.29–1.31	0.44–0.45	0.25	
20	12.7–13.3	5.6–6.0	1.26–1.28	0.42–0.43	0.24	
25	13.4–13.9	6.1–6.5	1.23–1.25	0.40–0.41	0.23	
30	14.0–14.5	6.6–7.0	1.20–1.22	0.38–0.39	0.22	
35	14.6–15.1	7.1–7.5	1.17–1.19	0.36–0.37	0.21	*pendula*
40	15.2–15.7	7.6–8.0	1.14–1.16	0.34–0.35	0.19–0.20	
45	15.8–16.3	8.1–8.5	1.11–1.13	0.32–0.33	0.17–0.18	
50	16.4–17.0	8.6–9.0	1.08–1.10	0.30–0.31	0.15–0.16	
55	17.1–17.7	9.1–9.5	1.04–1.07			
60	17.8–18.4	9.6–10.0	1.00–1.03			
65	18.5–19.1	10.1–10.6	0.96–0.99			↓
70	19.2–19.8					*n. vulgata*

umbilical region and shoulder of last whorl always with papillae; aperture square, dished; lip swelling thick; upper lip tooth broad and receding, located on right side of aperture; lower lip tooth medium large and marginal, located at or near middle of lower lip; parietal lamella of normal size, nearly straight.

Differential diagnosis. Triodopsis n. vulgata differs from *T. j. juxtidens* in that the upper lip tooth is broader and more receding, the whorls are more capacious, and the umbilicus is wider and more cylindrical. It is distinguished from *T. f. fallax* by its wide and cylindrical umbilicus, capacious whorls, and straight parietal lamella.

Distribution. Triodopsis n. vulgata occurs in a vast area from Ontario south to Alabama, and from the Mississippi River east to the Appalachian Mountains (Fig. 13). Isolated outposts occur in eastern Wisconsin, New York, Maryland, and North Carolina.

The *measured material* comes from the following localities: *Ontario*: Elgin County (ANSP); Essex County (MCZ). *Michigan*: Oakland, Wayne, and Washtenaw counties (ANSP); Ionia County (MCZ). *Washington, D. C. Virginia*: Lee County (ANSP). *West Virginia*: Ohio County (ANSP); Hampshire County (MCZ). *Ohio*: Guernsey, Erie, Franklin, Cuyahoga, Warren, and Adams counties (ANSP); Hamilton County (MCZ). *Indiana*: Dearborn and Crawford counties (ANSP); Kosciusko, Tippecanoe, and Marion counties (MCZ). *Illinois*: Gallatin County (MCZ). *Kentucky*: Trimble and Casey counties (MCZ). *North Carolina*: Cabarrus and Clay counties (ANSP); Knox, Monroe, and Jackson counties (MCZ). *Alabama*: Madison (2 samples) and Jackson counties (ANSP). A total of 37 samples, 1–25 specimens each, 231 specimens altogether.

Ecology. Triodopsis n. vulgata is widely distributed in the beech-maple and western mesophytic forests. It also penetrates the periphery of the oak-chestnut, mixed mesophytic and oak-pine forest regions (Fig. 13). The northern limits of its range more or less coincide with those of the beech-maple forests. The plant association may be the factor that determines the subspecies border.

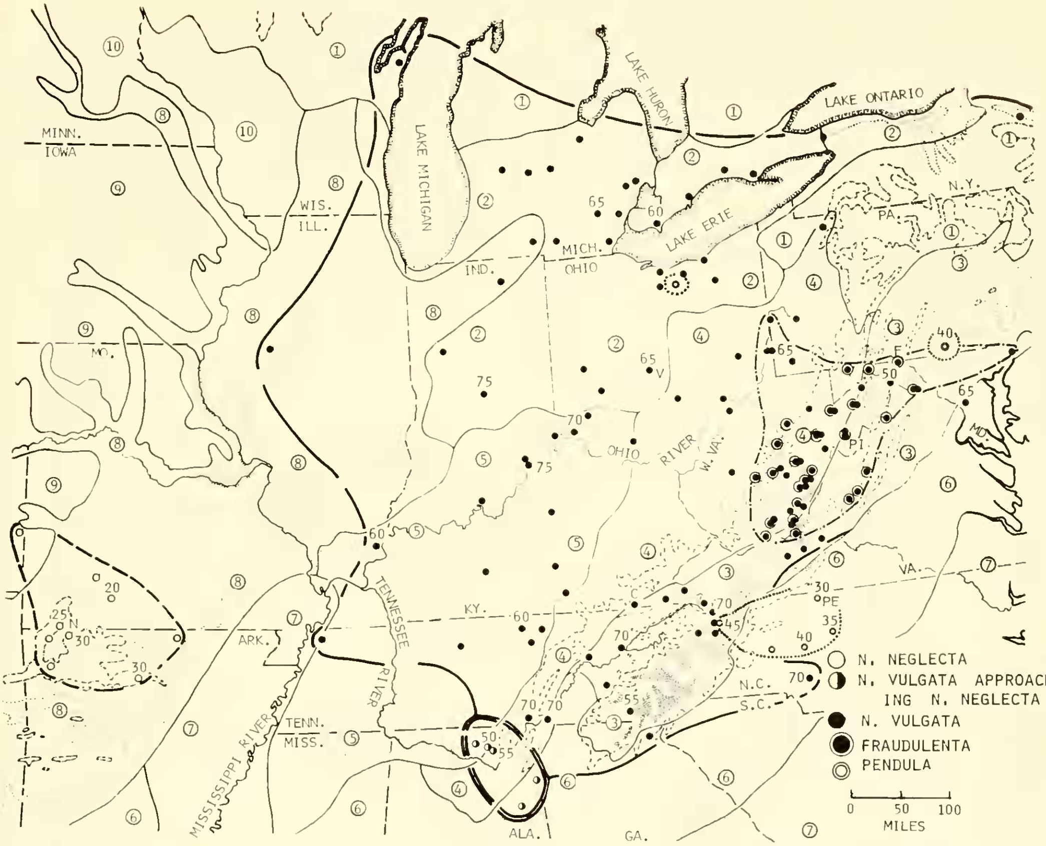


Figure 13. Distribution of *Triodopsis fraudulenta, neglecta,* and *pendula,* and the geographic variation of the character index in *neglecta* and *pendula.* Thick, solid line surrounds the range of *n. vulgata;* double, thick, solid line, *n. vulgata* approaching *n. neglecta;* thick, dashed line, *n. neglecta;* dotted line, *pendula;* dash-dot, *fraudulenta.* C, type locality of *claibornensis,* considered synonymous with *n. vulgata;* F, *fraudulenta;* N, *n. neglecta;* PE, *pendula;* PI, *picea,* considered synonymous with *fraudulenta;* V, *n. vulgata.* Numbers without a circle are mean values of samples in character index; samples of *n. neglecta* range from 20–30; *n. vulgata* approaching *n. neglecta,* 50–55; *n. vulgata,* 50–75; *pendula,* 30–40. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Most localities occur between 500 and 1500 feet (Fig. 13), but some lie at much lower or much higher elevations. Thus, one sample from Washington, D. C., comes from near sea level, another, from the Roan Mountains, Carter County, Tennessee, from 4000–5000 feet. Such high records are rare, however; on the whole, the subspecies does not seem to ascend as high as *T. fraudulenta* or *T. tridentata.*

Variation. The *aperture* varies only moderately. The separation of aperture grades, therefore, was not necessary.

Sculpture: The surface of the shell between the striae is covered with papillae. Fine spiral lines may replace the papillae on portions of the last whorl, but the umbilical and shoulder regions are always papillate. The papillae and the spiral lines intergrade; therefore, they can be considered homologous structures. The sculpture of *T. rugosa* shows similar intergradation.

Among the *measured characters,* shell width is correlated with height, umbilicus, and whorl number, not with the upper tooth to lower tooth ratio. All characters

TABLE V

MEASUREMENTS OF *TRIODOPSIS H. CLAIBORNENSIS*, AND OF REPRESENTATIVE POPULATIONS OF *T. N. VULGATA* AND *T. F. OBSOLETA*. THE ARROWS POINT TOWARD THE TAXON TO WHICH *CLAIBORNENSIS* SHOWS THE GREATER SIMILARITY IN THE CHARACTER IN QUESTION. BECAUSE OF THESE SIMILARITIES, AND ALSO BECAUSE OF ITS DISTRIBUTION, *CLAIBORNENSIS* IS CONSIDERED SYNONYMOUS WITH *N. VULGATA*.

			Mean of				
Name	Locality	Number of specimens	Width in mm	Height to width ratio	Umbilicus to width ratio	Whorl to width ratio	Upper to lower tooth ratio
n. vulgata	N. Carolina	6	13.5	0.51	0.21	0.40	1.15
n. vulgata types	Ohio	5	13.5	0.54	0.22	0.36	1.10
h. claibornensis type	Tennessee	1	12.7 ↑	0.54	0.19 ↑	—	1.20 ↓
f. obsoleta	N. Carolina	25	10.8	0.56	0.14	0.47	—
f. obsoleta	S. Carolina	5	11.4	0.54	0.15	0.47	1.20–1.25

show irregular geographic variation. It is remarkable that a form as widely distributed as *n. vulgata* has not developed any cline.

The mean values of population in character index also show moderate and irregular geographic variation (Fig. 13). All this evidence indicates that *n. vulgata* shows primary intergradation.

Systematics. Triodopsis n. vulgata is a widespread, common snail. Yet it somehow escaped description until as late as 1940. The partial reason for this delay may be that its conspecificity with a related form, *T. fraudulenta*, was taken for granted, and thus the workers could refer to it as *fraudulenta*; but the whole reason remains obscure to me. Northern and southern populations of *tridentata* were not named either, although one would have expected it because of their dissimilarity (p. 156).

As will be shown in later sections, *vulgata* is specifically distinct from *T. fraudulenta*, and probably conspecific with *T. neglecta*. For these reasons, and since *neglecta* is an older name than *vulgata*, it is necessary to change its name to *T. neglecta vulgata*.

Small, depauperate specimens of *T. n. vulgata* from Harrogate, Claiborne County, Tennessee, have been described by Lutz (1950) as *T. hopetonensis claibornensis*. They are not *hopetonensis*,[1] however, but *T. n. vulgata*, as shown by the comparison of some measurements (Table V). Also, *f. obsoleta* (= *hopetonensis*) does not occur anywhere near Harrogate, whereas *n. vulgata* does.

Triodopsis neglecta neglecta (Pilsbry) Plate II: 18–20

Polygyra neglecta Pilsbry, 1899, Nautilus 13: 40. Eureka Springs, Carroll County, Arkansas. Type ANSP 76283.

Triodopsis fallax Say, var. *minor* Wetherby, 1881, J. Cincinnati Soc. Nat. Hist. 4: 333. Springfield, Greene County, Missouri. *Non T. introferens* var. *minor* Tryon, 1867. Type not seen.

Definition. Triodopsis n. neglecta corresponds to *T. neglecta* of earlier authors. It contains those populations of the *fraudulenta* complex which have mean values between 20 and 30 in character index. The character index was prepared as shown in Table IV (p. 176).

Description. Shell width 9.9–13.2 mm, height 4.6–6.5 mm, height to width ratio 0.41–0.53; umbilicus 2.1–3.9 mm, umbilicus to width ratio 0.20–0.30; number of whorls 4.8–6.0, whorl to width ratio 0.40–0.51; upper tooth to lower tooth ratio 1.08–1.46;

[1] *Triodopsis hopetonensis* is considered hybrid between *T. f. alabamensis*, *f. fallax*, and *f. obsoleta* (p. 198). The taxon which Lutz called *hopetonensis* is here called *f. obsoleta* (p. 187).

embryonic whorls and sculpture as in *n. vulgata*; aperture square to trapezoid; lip swelling, lip teeth, and parietal lamella of moderate size; parietal lamella angular, pointing above upper lip tooth.

Differential diagnosis. Triodopsis n. neglecta differs from *T. n. vulgata* in that the shell is smaller, flatter, and more tightly coiled, the umbilicus wider and more cylindrical, the parietal lamella more angular, and the upper tooth to lower tooth ratio higher.

Distribution. Triodopsis n. neglecta occurs in the foothills of the Ozark Mountains, in Missouri and Arkansas. It is a peripheral isolate of *n. vulgata*, being separated from the latter by the Mississippi Valley (Fig. 13). There is a gap of about 150 miles between the closest *n. neglecta* and *n. vulgata* localities. The intervening area is not well collected, however, and new localities in this area may be discovered.

The *measured material* comes from the following localities: *Missouri*: Greene, Barry, and Christian counties (ANSP). *Arkansas*: Washington, Benton, Carroll, and Searcy counties (ANSP). *Kansas*: Bourbon County (2 samples). A total of 9 samples, 1–30 specimens each, 81 specimens altogether.

Ecology. Triodopsis n. neglecta is largely confined to the oak-hickory forest region (Fig. 13). Only a few localities occur outside of this region in the grasslands; probably, however, these localities also are woody patches, too small to show up on the map. The boundaries of the plant associations do not coincide with the subspecies border. Most localities lie between 500 and 1500 feet elevation.

Variation. There is only limited variation, as could be expected from the small distribution of the subspecies. The shell width is statistically correlated with height, umbilicus, and whorl number, as in other taxa of *Triodopsis*. All characters show irregular geographic variation.

Triodopsis n. vulgata populations approaching *Triodopsis n. neglecta*
Plate II: 15–17

The *neglecta* populations of Alabama resemble *n. vulgata* in size and apertural features, but resemble *n. neglecta* in height and umbilicus (Table VI). These populations are considered *n. vulgata* partly because their character index falls in the range of *n. vulgata* (Alabama populations: 50–55; *n. vulgata*: 50–75; *n. neglecta*: 20–30), partly because they occur near "normal" *n. vulgata* populations, isolated from *n. neglecta* (Fig. 13). Someone might wish to treat them, however, as intergrades between *n. vulgata* and *n. neglecta*. This would also be acceptable, but the former treatment is preferable, because of the reasons mentioned. Some populations from Tennessee also resemble *n. neglecta*, although to a lesser degree than do the Alabama populations.

The origin of these populations is probably reducible to simple variation. Hybridization is unlikely, because the range of variation in these populations is hardly greater than in the assumed "pure" parental populations (Fig. 4).

The Alabama and Tennessee populations are of great significance from a taxonomic point of view. They indicate that the genetic constitution of *n. vulgata* and *n. neglecta* is so similar that interbreeding between them would occur should they be in contact with each other. It therefore seems justified to consider the two forms conspecific. A similar case was encountered in *T. j. juxtidens* and *j. discoidea*.

Summary. (1) *Triodopsis neglecta* has two subspecies: *n. neglecta* and *n. vulgata*. The former was considered by earlier workers to be a separate species, the latter a subspecies belonging to *T. fraudulenta*. *Triodopsis n. vulgata* includes *T. hopetonensis claibornensis* as a synonym.

(2) *Triodopsis n. vulgata* is distributed over a vast area; *T. n. neglecta* is a peripheral isolate.

TABLE VI

RANGE OF VARIATION IN ALABAMA POPULATIONS OF *TRIODOPSIS N. VULGATA*. FOR COMPARISON, THE RANGE OF VARIATION OF *N. NEGLECTA* AND OF *N. VULGATA*, EXCLUSIVE OF THE ALABAMA POPULATIONS, IS ALSO SHOWN. ARROWS POINT TOWARD THE TAXON TO WHICH THE ALABAMA POPULATION BEARS THE GREATER SIMILARITY.

NAME	DISTRIBUTION	WIDTH IN MM	HEIGHT TO WIDTH RATIO	UMBILICUS TO WIDTH RATIO	UPPER TO LOWER TOOTH RATIO	CHARACTER INDEX
T. n. neglecta	Ozarks	9.9–13.2	0.41–0.53	0.20–0.30	1.08–1.46	20–30
			↑	↑		
variant *n. vulgata*	Alabama	14.6–16.8	0.46–0.51	0.24–0.29	1.09–1.16	50–55
		↓			↓	↓
T. n. vulgata exclusive of Alabama populations	Ontario to Tennessee	12.2–19.8	0.41–0.63	0.16–0.30	1.00–1.29	50–75

(3) Both subspecies prefer elevations of between 500 and 1500 feet. The northern limit of distribution of *T. n. vulgata* is probably determined by the northern boundary of the beech-maple association.

(4) Both subspecies show primary intergradation and irregular geographic variation; it is surprising that with such an extensive range *n. vulgata* has developed no cline.

Triodopsis pendula Hubricht
Plate II: 24–26

Triodopsis pendula Hubricht, 1952, Nautilus 65: 82. Summit of Hanging Rock Mountain, Hanging Rock State Park, Stokes County, North Carolina. Holotype ANSP 188293, paratypes ANSP 188294.

Definition. Triodopsis pendula is recognized here as defined by its author. It contains those populations of the *fraudulenta* complex which have mean values of 30–45 in character index.[1] The chart used for computing character index is shown in Table IV.

Description. Triodopsis pendula combines shell features of *T. n. vulgata* with apertural features of *T. n. neglecta*. Shell width 10.7–13.8 mm; height 5.5–7.2 mm, height to width ratio 0.50–0.59; umbilicus 2.0–3.2 mm, umbilicus to width ratio 0.19–0.25; whorl number 4.9–5.8, whorl to width ratio 0.41–0.49; upper tooth to lower tooth ratio 1.09–1.34; embryonic whorls and sculpture as in *n. vulgata*; aperture trapezoid, dished in region of upper lip tooth; lip swelling well developed, upper lip swelling deeply receding, lower marginal; upper lip tooth moderately broad, flat, sometimes bifid, lower lip tooth normal, located near columella; parietal lamella gently bent to slightly angular, pointing above upper lip tooth.

Differential diagnosis. Triodopsis pendula differs from *T. n. vulgata* in that the shell is smaller and the lower lip tooth closer to the columella (higher upper tooth to lower tooth ratio). From *T. n. neglecta* it is differentiated by its narrower umbilicus and the looser coiling of the shell; also, the last whorl behind the aperture is more than 1.5 times wider than the penultimate one in *pendula*, less than 1.5 times in *n. neglecta*. *Triodopsis pendula* may also be mistaken for *T. rugosa*. However, the aperture is dished, the lower lip tooth is closer to the columella, and the last whorl is wider in *pendula* than in *rugosa*.

Distribution. Triodopsis pendula occurs in three isolated areas, in North Carolina–Tennessee, in Pennsylvania, and in Ohio (Fig. 13). The Ohio record (MCZ 81499) is open to question, but may be true. The other two areas lie along the eastern and

[1] Two populations of *T. n. neglecta* also have mean values of 30. The overlap is caused by the fact that *pendula* resembles *n. neglecta* in apertural features utilized in making the character index. Notwithstanding this overlap in character index, the two forms can be safely distinguished.

northeastern periphery of the range of *n. vulgata*. This disjunct distribution pattern may indicate that the species is disappearing, or may be indicative of a hopping dispersal. Unfortunately, we have no proof either way.

The *measured material* comes from the following localities: *Pennsylvania*: Adams County (ANSP). *Ohio*: Lorain County (MCZ). *North Carolina*: Stokes (2 samples), Rowan, and Davidson counties (ANSP); Stokes and Catawba counties (JV). *Tennessee*: Carter County (ANSP). A total of 9 samples, 1–10 specimens each, 34 specimens altogether.

Ecology. *Triodopsis pendula* lives in mixed oak-pine, oak-chestnut, and beech-maple forests (Fig. 13). All localities lie between 500 and 1500 feet elevation, except the one in Tennessee, which comes from a higher altitude. At this locality, *pendula* appears to coexist with *n. vulgata*; at least the museum lot contains one specimen of *pendula* among several of *n. vulgata*.

Variation. As a consequence of the small population and limited distribution, the variation is restricted. The measured characters are statistically correlated with each other; the geographic variation is irregular.

Systematics. *Triodopsis pendula* is specifically distinct from *T. n. vulgata*, because it overlaps and apparently coexists with that form without interbreeding.

Summary. *Triodopsis pendula* is a monotypic species, with disjunct distribution, limited variation, and a small population.

Triodopsis fraudulenta (Pilsbry)
Plate II: 21–23

Polygyra tridentata var. *fraudulenta* Pilsbry, 1894, Proc. Acad. Nat. Sci. Philadelphia 46: 20, pl. 1, fig. 6. Morgan County, West Virginia, opposite Hancock, Maryland. Type ANSP 64725.

Triodopsis picea Hubricht, 1958, Trans. Kentucky Acad. Sci. 19: 73. Spruce Knob, Pendleton County, West Virginia. Holotype ANSP 202186, paratypes ANSP 202185.

Definition. *Triodopsis fraudulenta* combines the taxa formerly known as *T. f. fraudulenta* and *T. picea*; the former *f. vulgata* is excluded. A character index was not prepared for this species.

Description. Shell width 12.7–16.9 mm, height 6.7–9.0 mm, height to width ratio 0.45–0.63; umbilicus 1.9–3.9 mm, umbilicus to width ratio 0.15–0.24; number of whorls 5.2–6.1, whorl to width ratio 0.34–0.43; upper tooth to lower tooth ratio 0.96–1.22; embryonic whorls and sculpture as in *n. vulgata*; aperture oval-rectangular, lip swelling thick, lower lip swelling forming a straight edge; upper lip tooth very broad and deeply receding, located on right side of aperture; lower lip tooth narrower and marginal, located at middle of lower lip or closer to columella; parietal lamella large and nearly straight; lip teeth and parietal lamella usually overlap as one looks into the aperture; in a few specimens the lip teeth and parietal lamella do not overlap, and the upper lip tooth is less receding than usual.

Differential diagnosis. *Triodopsis fraudulenta* differs from *T. n. vulgata* in that the aperture is oval-rectangular, the lower lip swelling forms a straight ledge, the lip teeth and the parietal lamella are very large, the upper lip tooth is deeply receding, and the last whorl behind the aperture is only 1.2–1.6 times wider than the penultimate one. In *n. vulgata*, the aperture is usually square, the lower lip swelling does not form a straight ledge, the armature is weaker, the upper lip tooth is moderately receding, and the last whorl behind the aperture is 1.4–1.8 times wider than the penultimate.

Distribution. *Triodopsis fraudulenta* is found in the high mountain regions of Virginia and Maryland (Fig. 13). Its range lies on the periphery of that of *n. vulgata*, with ample overlap. Surprisingly enough, it is missing from the southern Appalachians; for explanation, see ecology, below.

The *measured material* comes from the following localities: *Maryland*: Garrett,

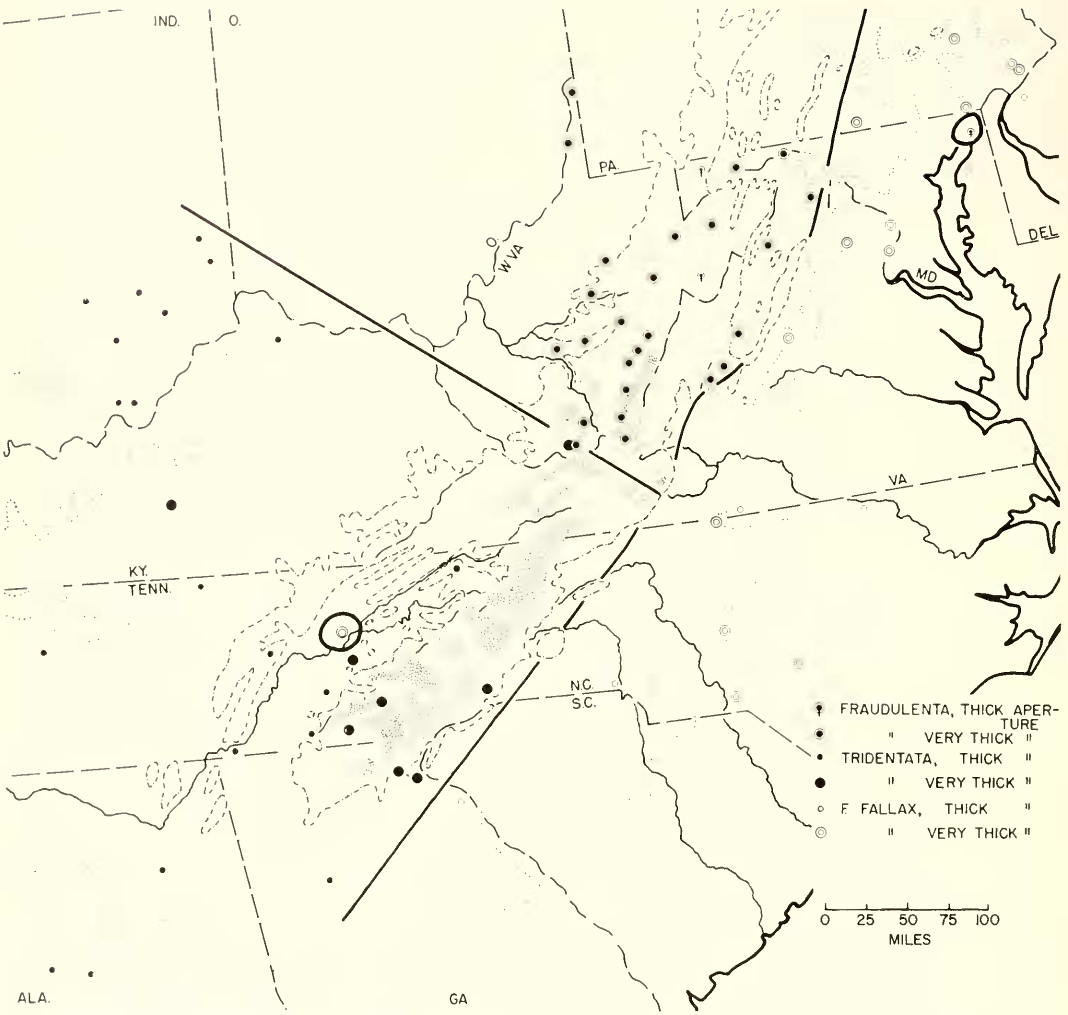


Figure 14. Distribution of *Triodopsis fraudulenta* and the mountain forms of *Triodopsis tridentata* and *Triodopsis f. fallax*. Thick, solid line separates the range of the three forms; there is almost no overlap. Other symbols refer to elevation and state boundaries, as explained in Figure 3.

Alleghany, and Cecil counties (ANSP). *Virginia*: Giles and Rockbridge counties (ANSP). *West Virginia*: Morgan (2 samples) and Pendleton counties (ANSP); Greenbrier County (MCZ). A total of 9 samples, 1–10 specimens each, 34 specimens altogether.

Ecology. *Triodopsis fraudulenta* is a mountain form of *T. n. vulgata*. It occurs between 1500 and 4000 feet, except for a few localities which lie outside these limits (Fig. 13). Thus, at Spruce Knob, Pendleton County, West Virginia, the snail reaches 4400 feet (*picea*, Hubricht, 1958), whereas in Morgan County, West Virginia, opposite Hancock, Maryland, it is found between 400 and 500 feet. It seems probable that the Potomac River and its tributaries washed the snail down to such low elevations. This mode of dispersal is observed also in *T. juxtidens*. Ironically, the lowland population had been found before other populations of *fraudulenta* were discovered, and thus became the type population.

The area occupied by *fraudulenta* is covered by mixed mesophytic and oak-chestnut forests, except for the higher peaks, which may reach up into the evergreen zone (Fig. 13). The distribution of the forest types and the snail are not correlated.

Triodopsis fraudulenta occurs only in the higher regions of the northern Appalachians. The comparable habitats in the southern Appalchians are occupied by the mountain-form, grade D, of the related species, *T. tridentata* (Fig. 14). It seems clear that the two forms exclude one another. Each form "fills" its habitat completely, thus leaving no room for the other.

Variation. Aperture: In the populations from Spruce Knob, Pendleton County, West Virginia, and Jennings, Garrett County, Maryland, the upper lip tooth is narrower and less receding than normal for *fraudulenta*, thus approaching *T. n. vulgata*. This may be caused by introgression from *n. vulgata*, but may be due to simple variation. A definite conclusion cannot be reached, because only two populations—six specimens—are available, not enough for statistical analysis. The Spruce Knob population has been described by Hubricht as *T. picea*.

The strong development of the lip swelling, lip teeth, and parietal lamella occurs in all species of the subgenus which inhabit higher mountains, *tridentata*, *rugosa*, *fraudulenta*, and *f. fallax*. These features appear to be adaptive, but their exact significance is unknown.

Measured characters: Shell width, height, umbilicus, and whorl number are correlated statistically. Their geographic variation is irregular.

Systematics. *Triodopsis fraudulenta* appears to be a specialized mountain form of *T. n. vulgata*. Thus it would seem logical to consider it conspecific with the latter, as earlier workers have indeed done. But the two forms seem to have reached reproductive isolation—they do not interbreed despite a wide overlap. For this reason, it is necessary to separate them on the species level. It may be added that partial ecological isolation also has been achieved, since *fraudulenta* prefers higher areas than does *n. vulgata*.

Triodopsis picea has a somewhat narrower umbilicus, and a narrower and less receding upper lip tooth than "normal" *fraudulenta* (Hubricht, 1958). Its author also claims that it is "unique in having papillae over the upper surface of the shell." On this basis, he ranks it as a full species. I believe this to be unwarranted. The measurements of *picea* are clearly within the range of *fraudulenta* (Table VII). The upper surface of the shell of *fraudulenta*, as well as of some other species of *Triodopsis*, is papillated. Only the differences in the aperture remain. When one considers, however, how much the aperture varies in *Triodopsis*, not much importance can be attributed to these relatively minor differences. The conclusion is thus that *picea* should not be separated from *fraudulenta* on a morphological basis. The same is true of distribution. Hubricht reported *picea* from Spruce Knob, Pendleton County, Three Forks of William River, Webster County, and Rainelle, Fayette County, all in West Virginia. A population from Jennings, Garrett County, Maryland, can also be included with the above. All these localities are isolated from one another, and lie within the range of *fraudulenta*. At no locality do *picea* and *fraudulenta* occur together.

Summary. (1) *Triodopsis fraudulenta* is a monotypic species, with *T. picea* as a synonym. The former *T. f. vulgata* is excluded from the species.

(2) *Triodopsis fraudulenta* is a specialized mountain form of *T. n. vulgata*. It occurs in the northern Appalachians, primarily at higher elevations. Similar regions in the southern Appalachians are occupied by the mountain form of the related spe-

Table VII

Measurements of *Triodopsis picea* and Two Populations of *T. fraudulenta*. The Former is Considered Synonymous with the Latter.

Name	Locality	Number of speci-mens	Mean of: Width in mm	Height to width ratio	Umbilicus to width ratio	Whorl to width ratio	Upper to lower tooth ratio
picea types	W. Virginia	3	14.0	0.56	0.17	0.39	1.07
fraudulenta	Maryland	3	15.2	0.55	0.17	0.35	1.09
fraudulenta types	W. Virginia	1	15.7	0.54	0.20	0.36	1.18

cies, *T. tridentata*. Thus the two mountain forms show ecological exclusion.

Evolutionary relationships within the fraudulenta complex. As the morphological and distributional evidence indicates, *T. n. vulgata* may be the central stock from which developed the other members of the complex, *n. neglecta*, *pendula*, and *fraudulenta*. This form is in intimate relationship with the others, and occupies a geographically central position as well. The other forms can be derived from *n. vulgata*, and occupy positions peripheral to *n. vulgata*. It thus seems likely that they once were part of the population of *n. vulgata*, but became isolated and diverged.

The *fallax* Complex

Definition. This complex contains two polytypic species with five subspecies: *T. fallax*, with subspecies *f. fallax*, *f. obsoleta*, and *f. alabamensis*; and *T. copei*, with subspecies *c. copei* and *c. cragini*; and one, somewhat isolated monotypic species, *T. soelneri*.

Triodopsis fallax (Say)
Triodopsis fallax fallax (Say)
Plate III: 4, 5, 10, 11

Helix fallax Say, 1825, J. Acad. Nat. Sci. Philadelphia 5: 119. Neotype selected by Pilsbry (1940: 809, fig. 480a). Manayunk, Montgomery County, Pennsylvania. Neotype ANSP 25821.

Helix introferens Bland, 1860, Ann. Lyc. Nat. Hist. New York 7: 117, pl. IV, figs. 3–4. Gaston County, and Salem, Forsyth County, both North Carolina. Type not seen.

Triodopsis introferens var. *minor* Tryon, 1867, Amer. J. Conch. 3: 51. ". . . the whole country east of the Rocky Mountains." Type not seen.

Definition. Triodopsis f. fallax corresponds to *T. fallax* of Pilsbry (1940). It contains those populations of the species which have mean values of 50–100 in character index A, and of 70–90 in character index B. The chart used for computing character index is shown in Table VIII.

Description. Shell width 10.1–15.5 mm; height 5.9–9.1 mm, height to width ratio 0.50–0.66; umbilicus 1.3–3.2 mm, umbilicus to width ratio, 0.12–0.22; number of whorls 5.0–6.4, whorl to width ratio, 0.38–0.56; embryonic whorls 1.4–1.5, with faint striation or almost smooth; subsequent whorls with more pronounced striae, last whorl with 3–5 strong striae per millimeter; intervals between striae smooth, papillae occurring only in umbilical region and behind aperture; aperture oval to auriculate, lip swelling thick, slightly receded, and therefore edge of aperture sharp; lip teeth large, upper lip tooth moderately to deeply receding, lower lip tooth marginal; a small or large fulcrum present inside last whorl; usually a small, flat projection present on face of lower lip.

Differential diagnosis. Triodopsis f. fallax is easily distinguished from *T. fraudulenta* because it has a fulcrum and a narrow umbilicus which expands suddenly at the last whorl. *T. fraudulenta* has no fulcrum, and its umbilicus is wide at the beginning, expanding moderately at the last whorl.

TABLE VIII

CHART FOR COMPUTING CHARACTER INDEX FOR *TRIODOPSIS FALLAX*.

Character Index A

SCORE	APERTURE GRADE	FULCRUM	
0	A	none	*f. obsoleta*
20	B	small	↑
40	C	large	↓
60	D	—	*f. fallax*

Method of calculation: A specimen having an aperture grade D and a large fulcrum is scored 60 + 40 = 100, the maximum possible score.

Character Index B

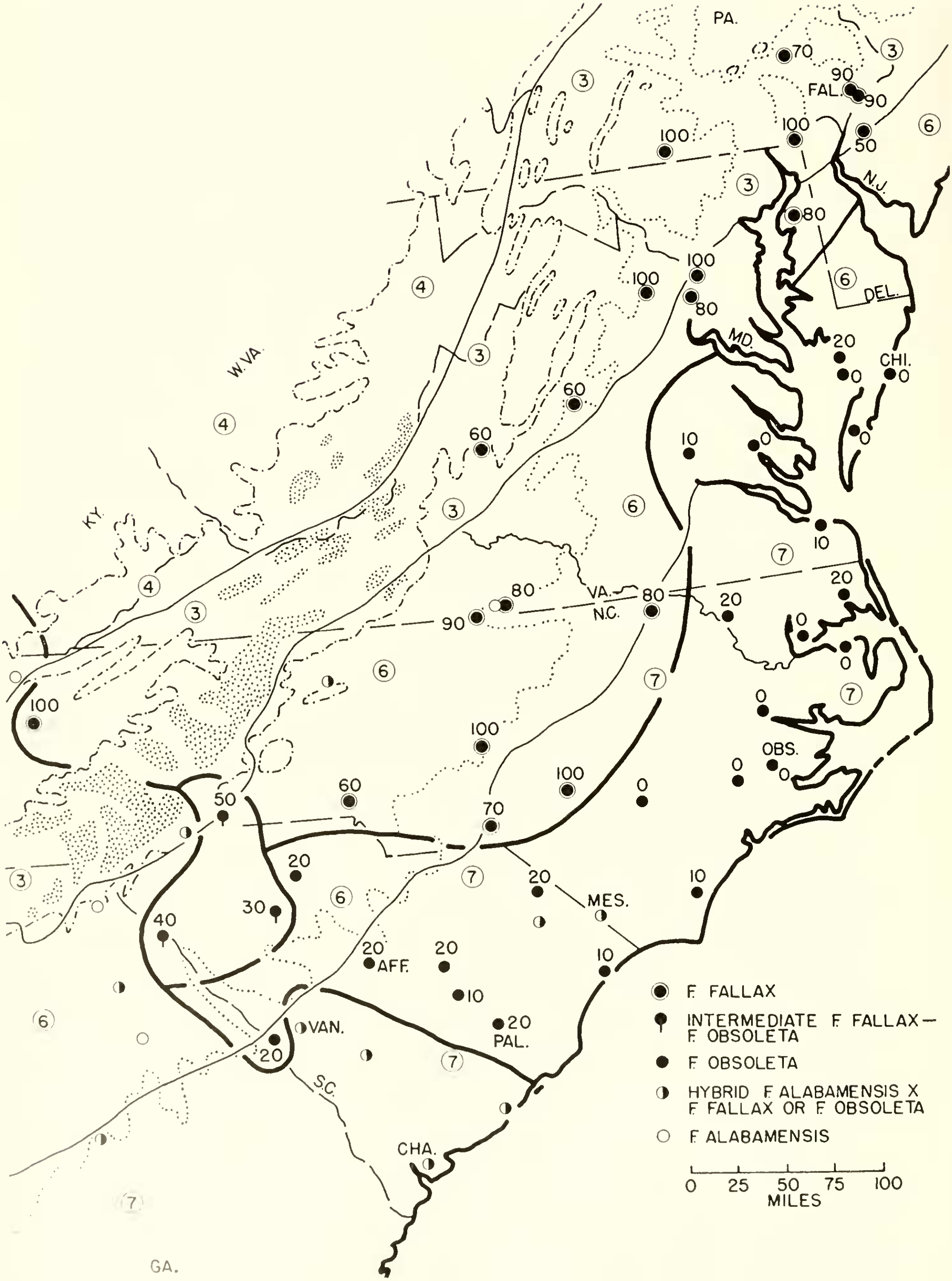
SCORE	WHORL TO WIDTH RATIO	ANGLE OF RIGHT SIDE OF APERTURE (IN DEGREES)	PARIETAL LAMELLA	EDGE OF APERTURE	
0	0.67–0.68	77.5–80.0	arcuate	swollen	
5	0.66	82.5–85.0			*f. alabamensis*
10	0.64–0.65	87.5			↑
15	0.63	90.0–92.5	slightly angular	slightly swollen	
20	0.61–0.62	95.0			
25	0.60	97.5–100.0			
30	0.58–0.59	102.5	sharply angular, straight, missing	sharp	
35	0.57	105.0–107.5			
40	0.55–0.56	110.0–112.5			
45	0.54				
50	0.53				
55	0.52				
60	0.50–0.51				
65	0.49				
70	0.47–0.48				
75	0.46				
80	0.44–0.45				
85	0.43				
90	0.41–0.42				↓
95	0.40				*f. fallax-*
100	0.38–0.39				*f. obsoleta*

Method of calculation: a specimen with a whorl to width ratio of 0.38, an aperture angle of 112.5 degrees, a sharply angular parietal lamella, and a sharp aperture edge is scored (100 + 40 + 30 + 30)/2 = 100, the maximum available score.

Distribution. Triodopsis f. fallax ranges from New Jersey to North Carolina. Westward, it reaches to the Blue Ridge Mountains, and in one place to Tennessee (Fig. 15). It overlaps *T. tridentata* slightly, *T. j. juxtidens* extensively.

The *measured material* comes from the following localities: *New Jersey*: Gloucester County (ANSP). *Pennsylvania*: Philadelphia, Montgomery, Berks, Chester, and Adams counties (ANSP). *Maryland*: Kent County (ANSP). *Virginia*: Alex, Fairfax, Prince William, Albermarle, Rockbridge, and Pittsylvania counties (ANSP). *North Carolina*: Rockingham, Gaston, Randolph, Richmond, Cumberland, and Warren counties (ANSP). *Tennessee*: Knox County (MCZ). A total of 20 samples, 2–30 specimens each, 187 specimens altogether.

Ecology. Triodopsis f. fallax inhabits mixed oak-pine and oak-chestnut forests (Fig. 15). It reaches from about 300 feet on the coastal plain to about 1500 feet in the Blue Ridge Mountains. It is probable that elevation, or factors associated with el-


PA.
FAL.
N.J.
DEL.
MD.
CHI.
W.VA.
KY.
VA.
N.C.
OBS.
MES.
AFF.
PAL.
VAN.
S.C.
CHA.
GA.
F. FALLAX
INTERMEDIATE F. FALLAX—F. OBSOLETA
F. OBSOLETA
HYBRID F. ALABAMENSIS X F. FALLAX OR F. OBSOLETA
F. ALABAMENSIS
0 25 50 75 100
MILES

evation, determines the subspecies border to a great degree. The forest boundaries do not have such a role.

It remains obscure to me why *T. f. fallax* fails to reach above 1500 feet in the Blue Ridge Mountains. Judged by its heavy armature, *f. fallax* is a "mountain-adapted" snail (p. 239), and we would thus expect to find it at high altitudes. Competition and exclusion are in all likelihood not responsible for its absence, since no other mountain-adapted species of *Triodopsis* occurs in the region. Perhaps we should not consider the heavy armature an adaptation to the mountains; in most other cases, however, this feature is certainly associated with mountainous habitats, and in the species *fallax*, the heavy armature is restricted to the subspecies which lives in the highest regions of the species range.

In my experience, *T. f. fallax* does not coexist with *T. j. juxtidens*, although they extensively overlap and both inhabit woods. The size of these animals is approximately the same, and so are their ecological requirements; both live in the litter layer and feed on decaying plant material and fungi. Hence there is competition and resulting habitat exclusion between them. The similarity in the ecological requirements is striking, if we consider the wide differences in morphology. The morphological and ecological differences have evidently evolved at very different rates. *Triodopsis f. fallax* also shows exclusion with *T. tridentata*, which it narrowly overlaps.

Systematics. The first description of the taxon *fallax* was given by Say in 1825. Mistakenly, however, his name was applied to another taxon, today known as *fraudulenta*, whereas the true *fallax* was called *introferens*, Bland, 1865. Tryon pointed out this error in 1867. Subsequently, *fraudulenta* was changed to *fallax*, *introferens* became synonymous with the latter, and the name *fraudulenta* was transferred to the proper taxon.

Triodopsis fallax intergrades and probably hybridizes with *T. obsoleta* and *T. v. alabamensis* (p. 195, names in old usage). For this reason, I consider it conspecific with these forms. Since *fallax* is the oldest of the three names, the proper name of this species is *T. fallax*, and the earlier *fallax* becomes the nominal subspecies of this species.

Triodopsis fallax obsoleta (Pilsbry)
Plate III: 1–3, 6, 7

Polygyra fallax obsoleta Pilsbry, 1894, Nautilus 7: 140. Newbern, Craven County, North Carolina. Type ANSP 57195.

Triodopsis hopetonensis subsp. *chincoteagensis* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia No. 3: Land Mollusca of North America, 1 (2): 813, fig. 480d. Chincoteague Island, Accomac County, Virginia. Type ANSP 151482.

Triodopsis fallax subsp. *affinis* Hubricht, 1954, Nautilus 68: 28. Columbia, Richland County, South Carolina. Paratype ANSP 190820.

Triodopsis palustris Hubricht, 1958, Trans. Kentucky Acad. Sci. 19: 74. Flood-plain of Santee River, 5.5 miles southwest of St. Stephens, Berkeley County, South Carolina. Holotype ANSP 202187 and paratypes ANSP 202188.

Definition. Triodopsis f. obsoleta combines *fallax obsoleta* or *hopetonensis obsoleta*, *h. chincoteagensis*, *f. affinis*, and *palustris* of earlier authors. It contains those populations of the species which have

←

Figure 15. Distribution and the geographic variation of character index A of *Triodopsis f. fallax*, *f. obsoleta*, and intermediates between the two subspecies. Solid, thick line separates the ranges of the three groups. AFF, type locality of *affinis*; CHI, *chincoteagensis*; OBS, *f. obsoleta*; PAL, *palustris* (these four forms are all combined in *f. obsoleta*). FAL, *f. fallax*. CHA, *charlestonensis*; MES, *messana*; VAN, *vannostrandi* (these three forms are considered hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta*, or intermediate between *f. fallax* and *f. obsoleta*). Numbers without a circle are mean values of samples in character index A; samples of *f. obsoleta* range from 0 to 20, intermediate between *f. obsoleta* and *f. fallax*, 30–50, *f. fallax*, 50–100. Note that *f. fallax* and *f. obsoleta* are sharply separated in the northern and middle parts of the range, intergrading in the south. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

mean values of 0–20 in character index A and 70–90 in character index B. The chart used for computing character index is shown in Table VIII (p. 185).

Description. Shell width 9.7–13.5 mm; height 5.1–8.8 mm, height to width ratio 0.47–0.65; umbilicus 1.2–2.7 mm, umbilicus to width ratio 0.11–0.22; number of whorls 4.5–6.0, whorl to width ratio 0.39–0.53; embryonic whorls 1.4–1.5, with faint striation or almost smooth; subsequent whorls with more pronounced striae, last whorl with 3–5 striae per millimeter; space between striae smooth, except in umbilical region and behind aperture, where covered with papillae; aperture auriculate, sometimes oval; lip swelling thin to moderately thick and slightly receded, thus edge of aperture sharp; lip teeth lacking, small, or medium sized, upper lip tooth at most moderately receded, lower lip tooth marginal; parietal lamella small and straight or moderately large and angular; fulcrum usually absent; flat projection on face of lower lip absent or very small.

Differential diagnosis. Triodopsis f. obsoleta differs from *f. fallax* in that the aperture is more auriculate, the lip teeth and parietal lamella smaller, the fulcrum smaller or absent. Also, it usually has relatively fewer whorls than *f. fallax*.

Distribution. Triodopsis f. obsoleta is distributed along the eastern seaboard from Delaware to Georgia. On the west it is adjacent to *f. fallax*. The two forms are sharply separated in the northern and middle regions, but intergrade in the southern region (Fig. 15).

The *measured material* comes from the following localities: *Maryland*: Somerset County (2 samples, ANSP). *Virginia*: Accomac, Northampton, Henrico, King William, and Norfolk counties (ANSP). *North Carolina*: Sampson, Camden, Chowan, Tyrell, Beaufort, Craven, Jones, Hanover, and Northampton counties (ANSP). *South Carolina*: Dillon, Horry, Sumter, Clarendon, Richland, Union, and Berkeley counties (ANSP). *Georgia*: Richmond County (MCZ). A total of 24 samples, 2–31 specimens each, 434 specimens altogether.

Ecology. Triodopsis f. obsoleta occurs in the lower regions of the southeastern coastal plain, up to about 300–400 feet, rarely to 500 feet (Fig. 15). Since the subspecies border runs predominantly parallel to the contour lines, elevation, or factors associated with it, seems to determine the distributional limits of the snail. The area is covered by mixed oak-pine and southeastern evergreen forests (Fig. 15). Both kinds of forests seem to be equally suitable habitats for the snail. Several records are known from offshore islands.

Triodopsis f. obsoleta shows habitat exclusion with *T. j. juxtidens*.

Systematics. The taxon *obsoleta* was originally assigned by its author as a subspecies to *Triodopsis fallax*. A few years later, however, he transferred it to *T. hopetonensis*, and this is how it became commonly known. The change was for the worse, however, since *hopetonensis* is not a valid name, the type population being a hybrid between *f. alabamensis* and *f. fallax* or *f. obsoleta*. Also, *obsoleta* and *fallax* intergrade (see p. 189), and therefore should remain in the same species. I propose, in consequence, to reinstate the original name, although not quite with the original content.

In contrast to the views set forth in this paper, Hubricht (1953: 120) and Grimm (*in litt.*) consider *T. obsoleta* and *T. hopetonensis* as two separate species. Their *T. obsoleta* is what I consider grade A (see below) of *T. f. obsoleta*, and their *T. hopetonensis* corresponds largely to my grade B of *T. f. obsoleta*. Hubricht argues that there are differences between these grades in aperture, size, height, umbilicus, and color. Grimm speaks of differences in height of the spire and luster of the shell. On the basis of extensive measurements and studies, I cannot confirm that any of these differences is diagnostic (Fig. 16, and Table IX). The two grades cannot be separated on distributional grounds either, because their areas overlap, and they frequently occur together in the same population. I feel it is justified, therefore, to combine these grades into the single taxon, *T. f. obsoleta*.

Hubricht (1953: 121) also stated that ". . . in December, a series of specimens of *T. obsoleta* from two localities and specimens of *T. hopetonensis* from two other localities were examined anatomically. In all the specimens of *T. obsoleta*, the penis was fully developed, but in the specimens of *T. hopetonensis* all had the penis very small and immature in appearance. This suggests that a factor in the reproductive isolation of these two species may be a difference in the breeding season." This conclusion seems to be at variance with Grimm's experiments (*in litt.*). The latter investigator repeatedly crossed *hopetonensis* and *obsoleta* in the laboratory, which, of course, he could not have done if the two forms had different breeding seasons.

Three forms, known as *T. hopetonensis chincoteagensis*, *T. fallax affinis*, and *T. palustris*, appear to belong to *f. obsoleta*. The detailed argument for this assignation is as follows.

Triodopsis h. chincoteagensis is supposedly characterized by its small size, narrow umbilicus, and reduced lip teeth. These features occur, however, in many *T. f. obsoleta* populations, and thus the morphological separation does not hold (Table IX). The form in question occurs on an offshore island in Virginia (Fig. 15), "isolated" from the mainland population. This fact might seem to justify its subspecific rank, but the failure of the population to achieve any appreciable morphological divergence seems to indicate that the isolation is incomplete or of very brief standing. And for these reasons, a subspecific separation of the population is unfounded.

Triodopsis palustris has a larger and flatter shell, and a wider umbilicus than do most specimens of *T. f. obsoleta*, although there is no gap between them (Table IX). Rather, *palustris* represents the extremes of the variation of *f. obsoleta*. This form has been reported from the flood plains of the Savannah and Santee rivers and from the Altamaha Swamp (Hubricht, 1958). It thus appears to be a feebly characterized polytopic form, which, I believe, should not be recognized taxonomically.

Triodopsis f. affinis, from South Carolina, differs from *T. f. obsoleta* in that some specimens (4 of 11) have a swollen peristome. Since the latter feature normally occurs in *T. f. alabamensis*, *affinis* appears to be hybrid between *f. obsoleta* and *f. alabamensis*. The contribution of the *f. alabamensis* genes is so small, however, that the mean value of the population in character index B, 70, is still within the range of *f. obsoleta*, 70–90; *T. f. alabamensis* has mean values of 20–40, hybrids, 45–65. For this reason, I consider *f. affinis* synonymous with *f. obsoleta*, and not a hybrid.

Hubricht, who described *f. affinis*, also changed his opinion on its status. In a recent letter he wrote: "*T. f. affinis* is a hybrid swarm between *T. fallax* and *T. alabamensis*." It seems to me more likely that *f. obsoleta* is the first parent, because it occurs next to the area of *affinis*, whereas *f. fallax* does not. Furthermore, *T. f. fallax* and *f. obsoleta* intergrade in South Carolina, the region in question, and thus it may well be that intergrades, rather than "pure" *f. obsoleta* or *f. fallax*, produced *f. affinis* by interbreeding with *f. alabamensis*. But the difference is really not important.

Populations intermediate between *Triodopsis f. fallax* and *f. obsoleta*

A few samples of *T. fallax* are intermediate between *f. fallax* and *f. obsoleta* in morphological characters. This is expressed by the mean values of these populations in character index A, which vary from 30 to 50; those of *f. fallax* are 50–100, of *f. obsoleta*, 0–20. These samples are also intermediate in their geographic position (Fig. 15).

TABLE IX

MEASUREMENTS OF REPRESENTATIVE POPULATIONS OF *TRIODOPSIS HOPETONENSIS CHINCOTEAGENSIS*, *T. H. OBSOLETA*, *T. F. AFFINIS*, AND *T. PALUSTRIS*. ALL THESE TAXA BELONG TO *F. OBSOLETA*. *TRIODOPSIS F. AFFINIS* SHOWS SOME RESEMBLANCE TO *T. F. ALABAMENSIS* IN APERTURAL FEATURES.

Name	Locality	Grade: Aperture	Grade: Fulcrum	No. of Specimens	Mean of: Width in mm	Mean of: Height to width ratio	Mean of: Umbilicus to width ratio	Character index: A	Character index: B
identified as *obsoleta*, but comes from type locality of *chincoteagensis*	Chincoteague Island, Accomac County, Virginia	A	–	30	10.8	0.55	0.14	0	85
obsoleta	Criesfield, Somerset County, Maryland	A	–	17	11.1	0.55	0.13	0	85
types of *obsoleta*	Newbern, Craven County, North Carolina	A, B	–	5	11.7	0.53	0.17	0	85
obsoleta	Chocowinity, Beaufort County, North Carolina	A, B	–	25	12.4	0.52	0.18	0	90
paratypes of *f. affinis*	Columbia, Richland County, South Carolina	B	–	11	11.4	0.56	0.16	20	70
types of *palustris*	St. Stephens, Berkeley County, South Carolina	B	–	3	13.7	0.50	0.19	20	80

These populations may either represent primary intergradation between *T. f. fallax* and *f. obsoleta*, or be hybrids between the two subspecies. The fact that the range of their variation is not significantly larger than that of samples from either "pure" subspecies indicates that the former assumption is true. The fact, however, that intermediate populations occur only in the south, whereas in the north *f. fallax* and *f. obsoleta* are sharply separated from one another, indicates hybridization (see p. 192). Because the amount of material at hand is rather small, the question cannot be finally settled.

Measured samples of the intermediate populations come from the following localities: *North Carolina*: Polk County (ANSP). *South Carolina*: Laurens County (ANSP). *Georgia*: Hart County (ANSP). A total of 3 samples, 2–13 specimens each, 26 specimens altogether.

These intermediate populations are significant in that they demonstrate the conspecificity of *f. fallax* and *f. obsoleta.*

The variation of Triodopsis f. fallax, f. obsoleta, and intermediates between them. Since the variation of *T. f. obsoleta* is in several respects a natural continuation of that of *f. fallax*, it is reasonable to discuss the variation of the two subspecies together.

Individual characters. Aperture: According to the development of the aperture, four phases can be distinguished, referred to as aperture grades A, B, C, and D (Plate III). In grade A, the lip swelling is thin, the lip teeth and parietal lamella are absent or small; the upper lip tooth, when present, is slightly receding; the parietal lamella, when present, is short and straight. In grade B, the lip swelling is moderately thick, the lip teeth moderately large, the upper one slightly receding; the parietal lamella is also moderately large, and usually broken at a sharp angle; the lip teeth and parietal lamella do not obstruct the aperture. In grade C, the lip swelling is thick, the lip teeth are large, the upper one wide and receding; the parietal lamella is large and angular; these structures obstruct the aperture considerably. In grade D, the lip swelling is very thick, the lip teeth very large, the upper lip tooth very wide and deeply receding; the parietal lamella is also very large and angular; the lip teeth and parietal lamella seem to touch or even overlap one another when one looks into the aperture. The variation of the aperture grades is continuous. Thus the numbers and limits of the grades are, to some extent, arbitrary; a different number of grades might be recognized by other investigators.

Specimens of grades A + B, and C + D commonly occur together in the same population, but grade B specimens also may be found occasionally in C + D populations, or C in A + B. Populations consisting of A, B, or A + B specimens form subspecies *f. obsoleta*; those consisting of C, D or C + D specimens, *f. fallax*; populations consisting of B + C specimens constitute the intermediates. It might be noted that grade B specimens have been identified as *hopetonensis*, and grade A specimens as *obsoleta*, by most workers in the field.

Grade A specimens occur in a wide zone along the seashore; grade B specimens in a somewhat higher zone, and grades C and D still higher. These zones, however, overlap widely. The geographic distribution of the four aperture grades thus reflects an underlying, gradual, change in the environment, primarily in elevation. This conclusion is taxonomically important, since it cautions against attributing diagnostic importance to minor variations in the aperture.

Fulcrum: According to the degree of development, three types can be distinguished: fulcrum absent, small, or large. The three types intergrade. Specimens without a fulcrum usually belong to aperture grades A or B, occasionally to C or D. A small fulcrum is common in grades C and D, rare in B. A large fulcrum is common in grades D and C, less common in B. Thus, the development of the armature and the fulcrum is correlated to some extent. Populations of specimens without a fulcrum form *f. obsoleta*; those composed of specimens with a small or large fulcrum are *f. fallax*; populations which combine specimens with a small fulcrum or without one are the intermediates.

Specimens without a fulcrum usually occur near the seashore, those with a large fulcrum in the higher regions. So far, the arrangement is roughly zonal. Specimens with a small fulcrum do not, however, occur zonally; instead, they are found in three isolated groups in the northern, middle, and southern parts of the range. Thus the geographic variation of the fulcrum is not quite concordant with that of the aperture.

Parietal lamella: This may be (1) small and straight, (2) sharply angular, (3) slightly angular, or (4) arcuate (Plate III). The small and straight lamella is actually a reduced form of the sharply angular type, of which only the distal portion remains. This type is characteristic of specimens of aperture grade A, in which the lip teeth are reduced as well. Among the three remaining types, the sharply angular parietal lamella is the most common; it prevails in all aperture grades except A. The slightly angular and arcuate types are common only in a few southern populations. This is possibly caused by gene flow from the southern subspecies, *f. alabamensis*, in which the arcuate type is dominant. The slightly angular types in these cases may be the product of the mixing of the sharply angular and arcuate types.

The small, straight, type occurs in areas

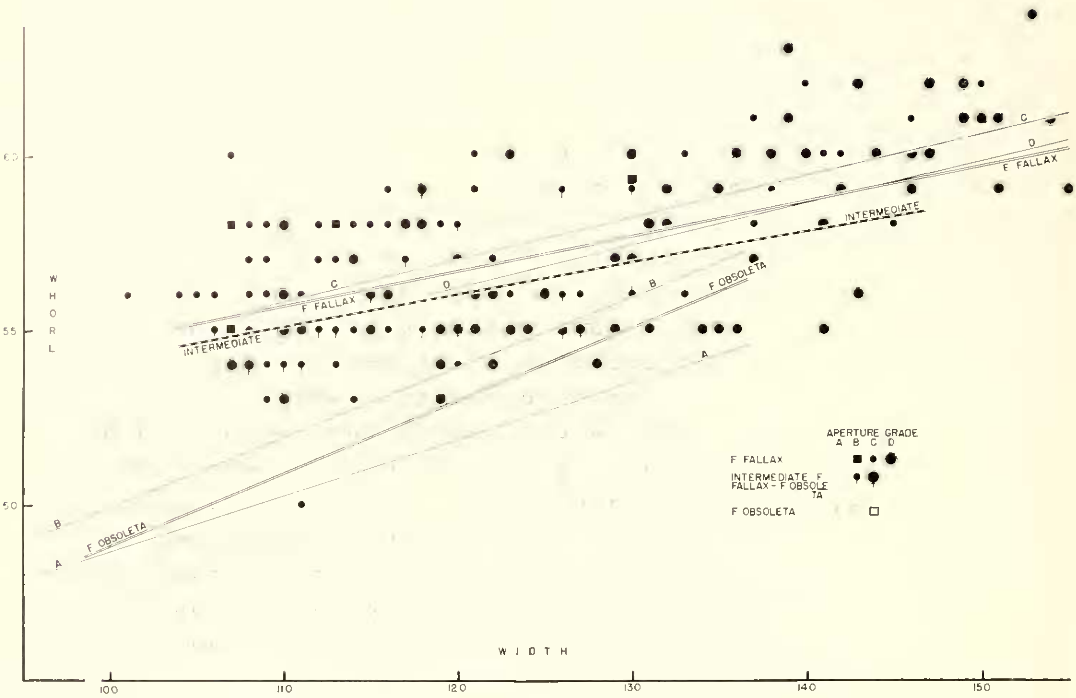


Figure 16. Scatter diagram of whorl number versus shell width in the four aperture grades of *Triodopsis f. fallax*, *f. obsoleta*, and intermediates between the two subspecies. The regression lines of whorl number on width show that aperture grade A is very close to B, and C to D, whereas B and C are farther apart. Scale of width in millimeters.

near the seashore; the sharply angular type prevails elsewhere, except for a few spots in the south where the slightly angular and arcuate types are also common.

Measured characters. The shell width is correlated with height, umbilicus, and whorl number. The regression lines of whorl number to width, calculated separately for the four aperture grades (Fig. 16), indicate closer relationships between grades A and B, and C and D, than between B and C. This is important from a taxonomic standpoint (p. 193).

The geographic variation of the measured characters is irregular. As an example, the variation of the whorl to width ratio is illustrated (Fig. 19, p. 197).

Character index: In the analysis of *T. f. fallax* and *f. obsoleta*, character index A is used. This is based upon a combination of the aperture and fulcrum grades (Table VIII, p. 185). It would, of course, have been better to use more than two characters. This could not be done, however, because the other characters overlap so widely that they would only confuse the situation, rather than clarify it.

The mean values of populations in character index A vary from 0 to 100. Populations with low mean values (*f. obsoleta*) are found near the Atlantic sea coast, those with high values (*f. fallax*) farther inland (Fig. 15). The transition from low to high mean values is gradual in the southern part of the range, but extremely sharp in the middle and northern parts.

This pattern might be what Huxley refers to as "widening of the hybrid belt" (1942: 250). According to this hypothesis, *f. fallax* and *f. obsoleta* were isolated from each other in an earlier period; recently, however, they re-established contact and started to hybridize. The hybrids are inferior to the parents; they are therefore selected against. Since the hybridization presumably started in the northern part of the range earlier than in the southern, the hybrids have been completely eliminated from the north, but still remain in the south. The absence of the hybrids makes the transition in character index sharp, their presence makes it gradual.

This theory sounds appealing, but it remains mere speculation until we can prove that the intergrading populations of the south are really hybrids, and that the hybrids are of inferior viability. Unfortunately, the available material is too limited for statistical analysis, and no experiments have been done on the viability of the hybrids. Other possible explanations also suffer from lack of evidence; thus there is, at present, no satisfactory explanation of the above phenomenon.

The geographic variation of character index A provides the foundation upon which the classification put forth in this paper rests (Fig. 15). It is argued here that only two taxa should be separated in the *fallax-obsoleta* group (excluding *f. alabamensis*), and the separation should be on the subspecies level. The geographic variation of character index A shows two groups of populations, one with low and another with high mean values, and it also shows that the two groups intergrade in the south. Other evidence comes from a study of the aperture, and of some metric characters, such as whorl number and width (Fig. 16), which also show the existence of two subspecies, one combining aperture grades A and B, the other, C and D.

The finding that *f. fallax* and *f. obsoleta* behave as subspecies in certain areas of the range, and as distinct species in others, is of great theoretical interest, since it shows that isolating mechanisms between two populations can develop at different rates in different parts of the range. The populations involved are actually neither species nor subspecies, but intermediate.

Triodopsis fallax alabamensis (Pilsbry)
Plate III: 9, 14, 15

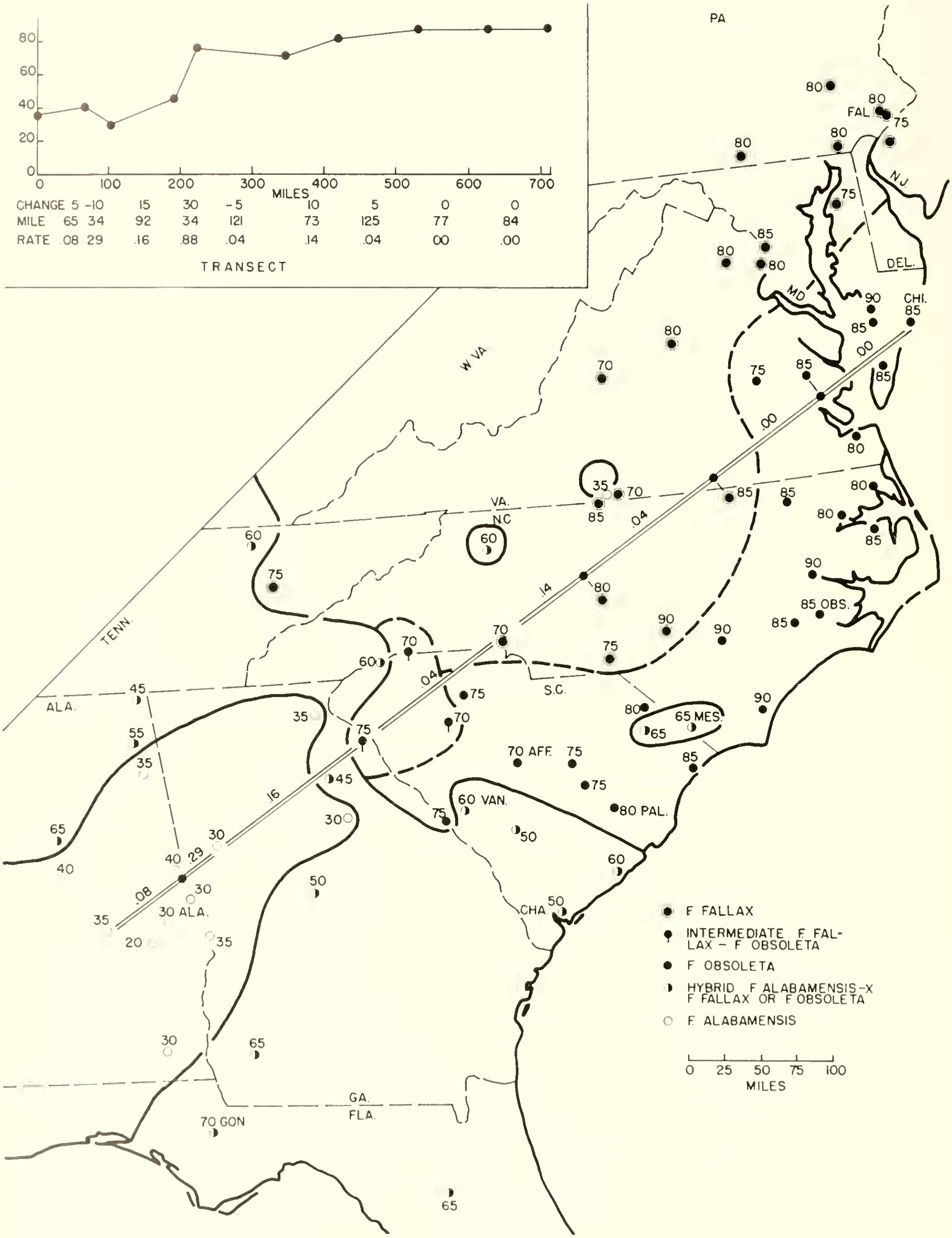
Polygyra alabamensis Pilsbry, 1902, Nautilus 16: 30. Elamville, Barbour County, Alabama.

Definition. *Triodopsis f. alabamensis* corresponds to *T. vannostrandi alabamensis* of earlier authors. It contains those populations of the species which have mean values of 20–40 in character index B. The chart used in computing character index B is shown in Table VIII (p. 185).

Description. Shell width 8.6–13.1 mm; height 4.9–7.5 mm, height to width ratio 0.48–0.66; umbilicus 1.2–3.0 mm, umbilicus to width ratio 0.12–0.24; number of whorls 5.1–7.0, whorl to width ratio 0.49–0.68; embryonic whorls 1.4–1.5, nearly smooth to finely striated; subsequent whorls with increasingly stronger striae; last whorl with 3–4 strong striae per millimeter; aperture square to trapezoid, slightly depressed; lip swelling medium thick, marginal, thus edge of aperture swollen; lip teeth medium large, upper lip tooth slightly receding; lower lip tooth marginal; parietal lamella arcuate or slightly or sharply angular; no projection on face of lower lip swelling.

Differential diagnosis. *Triodopsis f. alabamensis* is distinguished from *f. fallax* and *f. obsoleta* by its tighter coiling, square aperture, and swollen peristome. The latter two subspecies have looser coiling, an auriculate aperture, and a sharp peristome. From *T. c. cragini*, another similar form, it is separated by its greater number of whorls, and its smaller and less broad upper lip tooth.

Distribution. *Triodopsis f. alabamensis* occurs in eastern Alabama and northern Georgia (Fig. 17). It is also known from Danville, Pittsylvania County, Virginia, collected by Hubricht (misidentified as *T. f. affinis*). There is a sample of *f. alabamensis* in the collection of the ANSP from Jackson County, Texas, identified as *T. cragini* (ANSP 186723, collected by Cheatum). If my identification is correct, this locality is erroneous. Only *T. c. copei* and *T. c. cragini* occur in Texas.



80
60
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MILES
CHANGE 5 -10 15 30 -5 10 5 0 0
MILE 65 34 92 34 121 73 125 77 84
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TRANSECT
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TENN.
S.C.
ALA.
30 ALA.
GA.
FLA.
CHA
70 AFF.
60 VAN.
80 PAL.
65 MES.
85 OBS.
70 GON
F FALLAX
INTERMEDIATE F FAL-LAX – F OBSOLETA
F OBSOLETA
HYBRID F ALABAMENSIS-X F FALLAX OR F OBSOLETA
F ALABAMENSIS
0 25 50 75 100
MILES

The *measured material* comes from the following localities: *Virginia*: Pittsylvania County (ANSP). *Georgia*: Habersham, Greene, Coweta, and Muscogee counties (MCZ). *Alabama*: Randolph, Chambers, Lee (2 samples), Elmore, and Shelby counties (ANSP); Cherokee, Lee, Macon, and Dale counties (MCZ). A total of 15 samples, 2–27 specimens each, 144 specimens altogether.

Ecology. Triodopsis f. alabamensis occurs in mixed oak-pine and southeastern evergreen forests. In elevation, it ranges from a few hundred to about 1500 feet. Neither the plant associations nor the elevation play a major role in determining the distributional borders of the subspecies, except in the northwest, where the subspecies border closely follows the boundaries of the mixed oak-pine forests.

Variation. The *aperture* shows moderate variation. The lip teeth of most specimens correspond in size to those of aperture grade B of the *f. fallax-f. obsoleta* group. Occasional specimens with smaller lip teeth also occur. The *fulcrum* is absent, except in a single specimen from Auburn, Lee County, Alabama, which, incidentally, is the type locality of the subspecies. The occurrence of a specimen with a fulcrum at this locality is probably due to "introgression."

The *parietal lamella* may be arcuate, sharply angular, slightly angular, or small and straight. The frequencies of these types are 39, 22, 26, and 13 per cent, respectively. The arcuate type is somewhat more frequent in the southern areas than in the northern.

Among the *measured characters*, shell width is correlated with height, umbilicus, and whorl number. All characters, including the graded ones, show irregular geographic variation; in a small area like that of *f. alabamensis* one cannot really expect any trend in geographic variation to develop.

Systematics. Triodopsis f. alabamensis was originally ranked by its author as a full species. The same investigator later ranked it, however, as a subspecies of *T. vannostrandi* (Pilsbry, 1912). This was a bad move, since *vannostrandi* is a hybrid between *alabamensis* and *f. fallax* or *f. obsoleta*, and is, therefore, an invalid name. Correctly, we should combine *alabamensis* with *fallax*, since they freely hybridize. Evidence for this statement is given below.

Hybrid populations between *f. alabamensis* and the *f. fallax-f. obsoleta* group
Plate III: 8, 12, 13

Populations from the transitional zone between *f. alabamensis*, *f. fallax*, and *f. obsoleta* have mean values of 45–65 in character index B; that is, values intermediate between those of *f. alabamensis* (20–40) and *f. fallax* or *f. obsoleta* (70–90). One population from Blountstown, Calhoun County, Florida, with a mean value of 70, is also listed among the intermediate populations, because of its geographic position.

These samples are considered hybrids between *f. alabamensis* and the *f. fallax-f. obsoleta* group. This view is supported by the facts that they are morphologically and geographically intermediate, and their variation is greater than that of samples taken

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←

Figure 17. Distribution and the geographic variation of character index B of *Triodopsis fallax*. Thick, dashed line separates the ranges of *f. fallax*, *f. obsoleta*, and intermediates between the two subspecies; thick, solid line surrounds the range of *f. alabamensis* and hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies. Parallel, thin lines indicate a transect; thin, dashed lines are state boundaries. AFF., type locality of *affinis*; CHI., *chincoteagensis*; OBS., *f. obsoleta*; PAL., *palustris* (these four forms are all combined in *f. obsoleta*). FAL., *f. fallax*; ALA., *f. alabamensis*. CHA., *charlestonensis*; GON., *goniosoma*; MES., *messana*; VAN., *vannostrandi* (these four forms are all considered hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies). Numbers are mean values of samples in character index B. Samples of *f. alabamensis* range from 20 to 40, hybrid, 45–65, *f. fallax* and *f. obsoleta*, 70–90, intermediate between the latter two subspecies, 70–75.

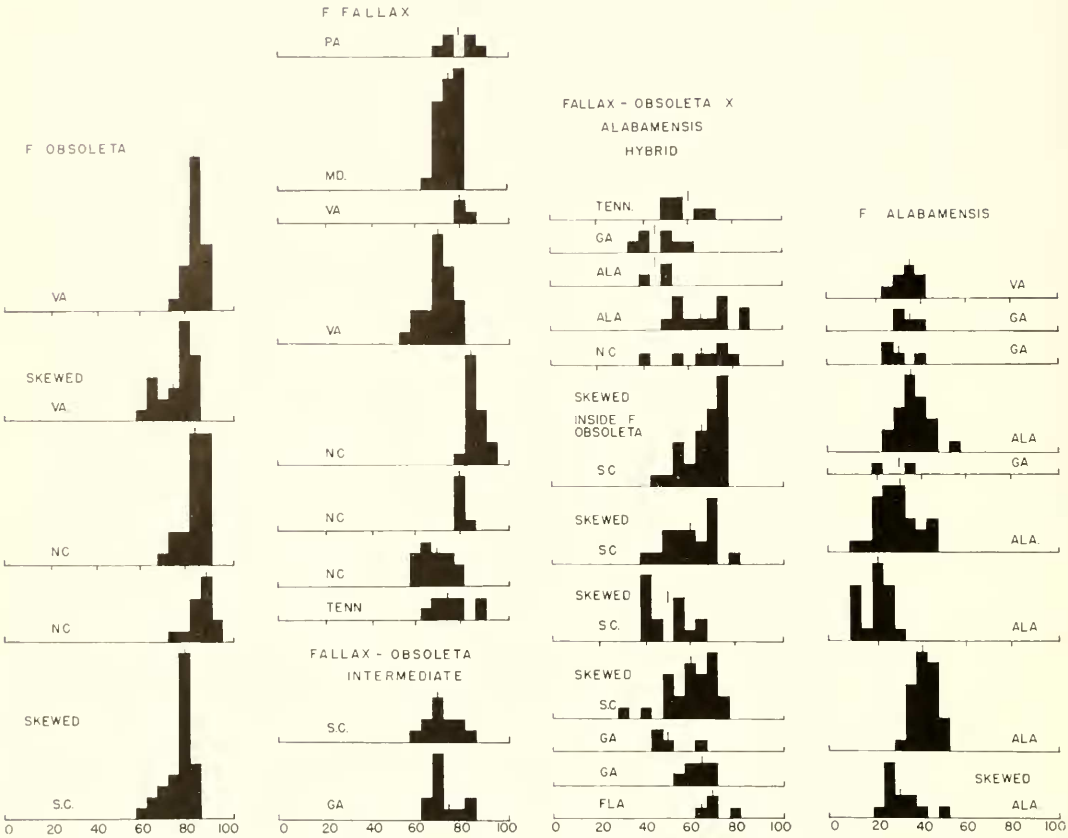

Figure 18. Character index B, histogram of samples of *Triodopsis fallax*. Short line on top of column indicates mean value of sample. The histograms of many hybrid samples are strongly skewed, those of the parental ones, normal or slightly skewed. The hybrid samples have a wider range of variation than do the parental samples. Samples of *f. alabamensis* also have a somewhat wider variation than do those of *f. fallax* or *f. obsoleta*. Scale in character index units. The abbreviations stand for the states where the samples have been collected.

from either of the putative parents (Figs. 4, 18, 26, 27).

The hybrid origin of the intermediate populations is further supported by the fact that the hybrid zone does not coincide with obvious changes in ecological factors, such as vegetation, elevation, temperature, humidity, or soil.

Hybrid populations have been *measured* from the following localities (Fig. 17): *North Carolina*: Wilkes and Columbus counties (ANSP). *Tennessee*: Campbell County (ANSP). *South Carolina*: Greenville County (MCZ); Aiken (2 samples), Bamberg, Marion, Charleston, and Beaufort counties (ANSP). *Georgia*: Clarke, Bibb, and Baker counties (MCZ). *Alabama*: Jackson County (MCZ); DeKalb and Jefferson counties (ANSP). *Florida*: Alachua and Calhoun counties (ANSP). A total of 18 samples, 1–30 specimens each, 162 specimens altogether.

The hybridization of *f. alabamensis* with *f. fallax* and *f. obsoleta* has several important effects on the taxonomy and nomenclature of the group. First, the former *T. alabamensis* must be considered conspecific with *f. fallax* and *f. obsoleta*. Second, the name *vannostrandi alabamensis* must be changed to *fallax alabamensis*. Third,

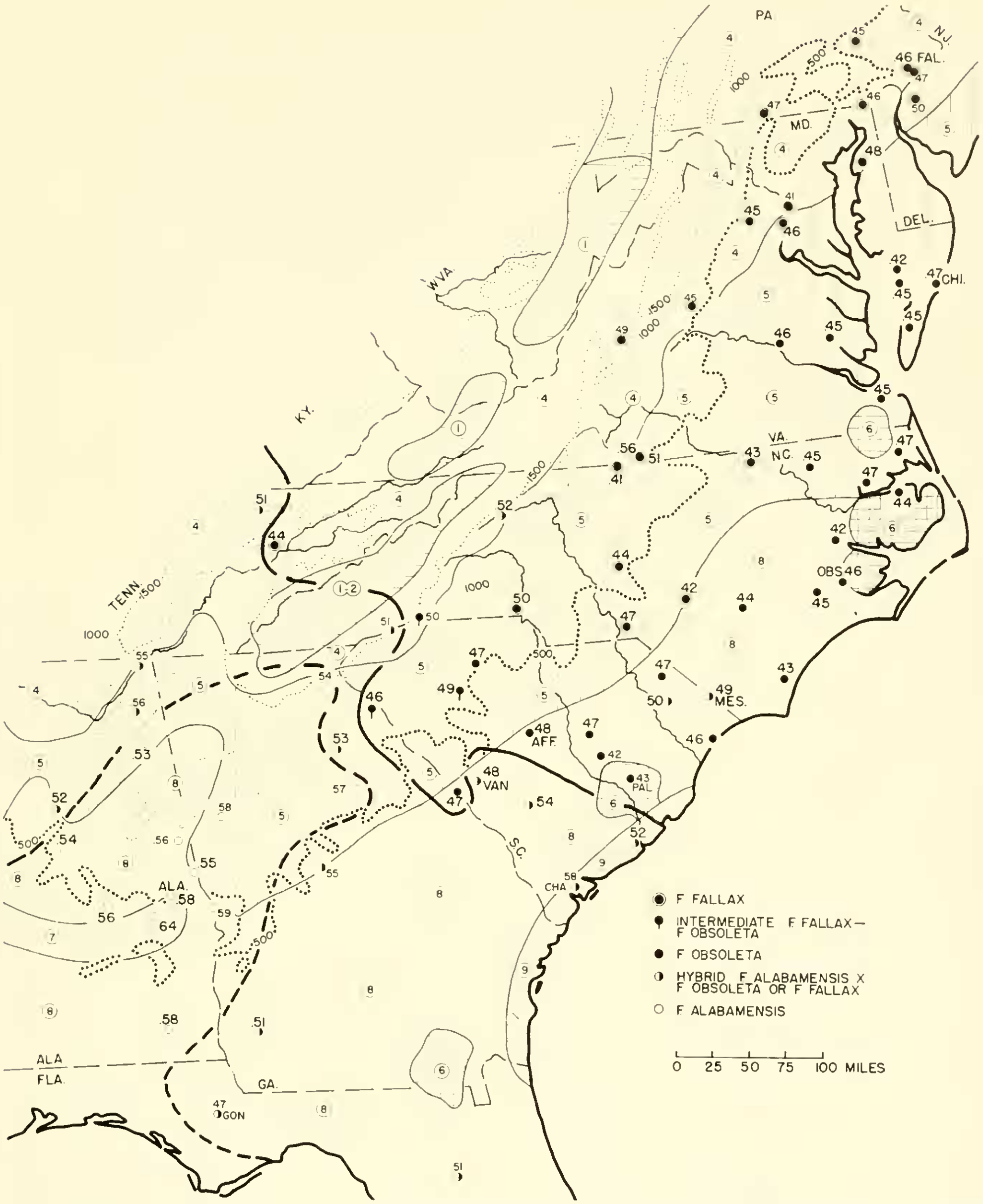

Figure 19. Geographic variation of whorl to width ratio in *Triodopsis fallax*. Thick, solid line separates the range of *f. fallax* and *f. obsoleta* from that of hybrid *f. alabamensis* × *f. fallax* or *f. obsoleta* or intermediates between the latter two subspecies; thick, dashed line separates the hybrids from *f. alabamensis*. Numbers without a circle are mean values of samples in whorl to width ratio; the samples of *f. fallax* range from 0.41 to 0.51; *f. obsoleta*, 0.42–0.48; intermediate, 0.46–0.50; hybrid, 0.47–0.58; *f. alabamensis*, 0.53–0.64. The variation of the character is irregular in all taxa. Numbers encircled refer to forest types (terminology after Fenneman, 1938): one, mainly coniferous forest; two, beech, birch, maple; four, chestnut, chestnut-oak, poplar; five, oak and pine; six, cypress, tupelo, red gum, river bottom forest; seven, prairie grassland with wooded valleys; eight, southeastern pine forest; nine, marsh grassland. Notice the "straits" of deciduous forests, chestnut, chestnut-oak, and poplar, between the "islands" of mainly coniferous forests; the former provided convenient routes of dispersal for several species of *Triodopsis* (p. 167). Elevation: • • • • • 500-foot contour line; ······ 1000-foot; · · · · · 1500-foot. Other symbols and abbreviations as in Figure 17.

the names previously given to the hybrid populations must not be used. There are five such names:

Helix hopetonensis Shuttleworth, 1852, Mitt. Naturforsch. Ges. Bern No. 248: 198. Hopeton, near Darien, Georgia. Cotype MCZ 18225.

Helix vannostrandi Bland, 1875, Ann. Lyc. Nat. Hist. New York 11: 200. Aiken, Aiken County, South Carolina. Type not seen. Topotypes ANSP 57196 and 86104.

Polygyra fallax subsp. *goniosoma* Pilsbry, 1912, Nautilus 26: 80. In oak and pine-woods, Blountstown, Calhoun County, Florida. Type ANSP 77948.

Polygyra hopetonensis var. *charlestonensis* Mazyck, 1913, Contrib. Charleston Mus. 11: 7. Charleston, Charleston County, South Carolina. Type ANSP 106850.

Triodopsis messana Hubricht, 1952, Nautilus 65: 80. Whiteville, Columbus County, North Carolina. Holotype ANSP 187456, paratypes 187455.

Hubricht (1953, *in litt.*) states that *fallax, hopetonensis, obsoleta* and *alabamensis* are separate species, isolated from one another by "geographical and ecological" factors or by a difference in the breeding season, and only hybridize where their natural habitats have been destroyed. He also stated that hybrid populations are only found in "disturbed" habitats, like vacant lots. From these observations he concluded that, "Prior to the coming of the white man to America, it is doubtful if they ever hybridized."

On the distributional map of the group (Figs. 15, 17) one cannot see any obvious geographic barrier between *f. fallax* and *f. obsoleta* or *f. alabamensis*. Hubricht also failed to tell where they are supposed to be. Ecological isolation may exist between *f. fallax* and *f. obsoleta*, but it is unlikely between these and *f. alabamensis*. The hybrid populations occur not only in disturbed habitats, but also in relatively undisturbed ones, such as national forests and state parks. In such habitats, "pure" populations are found outside of the hybrid zone. Furthermore, it is unlikely that habitat disturbance would occur only in the Georgia-Carolina region, where hybrids are found, and not in the Maryland-Washington-Virginia region, where *f. fallax* and *f. obsoleta* are sharply separated from one another. For all of these reasons, it seems doubtful to me that habitat disturbance is the only or even the major factor in the hybridization of the *fallax* group, although it may have helped to facilitate it.

Evolutionary relationships. Triodopsis f. fallax is most closely related to *f. obsoleta*. *Triodopsis f. alabamensis*, judged on a morphological basis, was separated from the *fallax-obsoleta* stock a long time ago; it has failed, however, to achieve reproductive isolation, and is therefore presently merging with this stock.

Summary. (1) *Triodopsis fallax* consists of three subspecies: *f. fallax*, *f. obsoleta* and *f. alabamensis*. The first corresponds to *T. fallax* of contemporary authors. The second combines the former *hopetonensis obsoleta*, *h. chincoteagensis*, *fallax affinis* and *palustris*. The third corresponds to the former *vannostrandi alabamensis*.

(2) *Triodopsis f. fallax* and *f. obsoleta* intergrade in the southern part of the range, but are sharply separated elsewhere (this may be the phenomenon referred to as "widening of the hybrid belt"). Because of this intergradation, *fallax* and *obsoleta* are considered conspecific; they both freely hybridize with *f. alabamensis*—a proof of conspecificity with that form. Habitat disturbance by man probably did not play a major role in initiating the hybridization.

(3) Judged by its heavy armature, *f. fallax* appears to be a mountain snail; in fact, however, it occurs at relatively low elevations. The reason for this anomalous distribution is not known.

(4) *Triodopsis f. fallax* and *f. obsoleta* are ecologically exclusive of *T. tridentata* and *T. j. juxtidens*.

(5) The geographic variation of most characters is irregular in all three subspecies. The aperture varies clinally, however,

TABLE X

CHART FOR COMPUTING CHARACTER INDEX FOR *TRIODOPSIS COPEI*. METHOD OF CALCULATION: A SPECIMEN HAVING A WIDTH OF 14.5 MM, AN UMBILICUS OF 3.5 MM, A WHORL TO WIDTH RATIO OF 0.42, AN APERTURE GRADE D, AND A LARGE FULCRUM SCORES (50 + 30 + 40 + 40 + 40)/2 = 100, THE MAXIMUM POSSIBLE SCORE.

SCORE	WIDTH IN MM	UMBILICUS IN MM	WHORL TO WIDTH RATIO	APERTURE GRADE	FULCRUM GRADE	
0	7.7–8.2	1.1–1.4	0.58–0.60	B	none	*c. cragini* ↑
5	8.3–8.7	1.5–1.8	0.56–0.57			
10	8.8–9.3	1.9–2.2	0.54–0.55	B-C	questionable	
15	9.4–9.9	2.3–2.5	0.52–0.53			
20	10.0–10.5	2.6–2.8	0.50–0.51	C	small	
25	10.6–11.1	2.9–3.2	0.48–0.49			
30	11.2–11.7	3.3–4.0	0.46–0.47			
35	11.8–12.2		0.44–0.45			
40	12.3–12.8		0.41–0.43	D	large	
45	12.9–13.4					
50	13.5–14.5					↓ *c. copei*

from *f. fallax* to *f. obsoleta*, and this cline corresponds to gradual changes in the environment, primarily in elevation. There is no clinal variation in *Triodopsis f. alabamensis*.

(6) *Triodopsis f. fallax* and *f. obsoleta* are very close relatives. Long ago, presumably, *Triodopsis f. alabamensis* split away, but is presently fusing with them.

Triodopsis copei (Wetherby)

The name *Triodopsis copei* supersedes the more commonly used *T. vultuosa*, for reasons to be explained below. Two hybridizing subspecies belong to the species: *c. copei* and *c. cragini*.

Triodopsis copei copei (Wetherby) Plate III: 20

Helix copei, or *H. vultuosa* var. *copei* Wetherby, 1878, Amer. Nat. 12: 185. Twenty miles north of Beaumont, Jefferson County, Texas. Types ANSP 57222 and 82316.

Definition. *Triodopsis c. copei* is the former *T. vultuosa copei*. The populations that belong to this subspecies have mean values of 75–100 in character index. The method of computing character index is described in Table X.

Description. Shell width 11.5–14.5 mm; height 6.1–7.5 mm, height to width ratio 0.48–0.60; umbilicus 1.9–4.0 mm, umbilicus to width ratio 0.17–0.28; number of whorls 5.3–6.0, whorl to width ratio 0.41–0.50; embryonic whorls 1.4–1.5, with faint striation below suture; striation becoming more pronounced on later whorls, 3–5 striae per millimeter on last whorl; intervals of striae without papillae; aperture trapezoid, square, oval, or rarely auriculate; lip swelling thick and marginal or very slightly receding, therefore edge of aperture swollen; upper lip tooth very broad and deeply receding, lower lip tooth moderately large and marginal, often buttressed on its left side; parietal lamella large and angular; fulcrum moderate to large; moderate to large projection on face of lower lip.

Differential diagnosis. *Triodopsis c. copei* is very similar to *T. f. fallax*. The best distinction between them is that *c. copei* has a swollen peristome and a moderate to large projection on the lower lip, whereas *f. fallax* has a sharp peristome and a small projection.

Distribution. *Triodopsis c. copei* is known only from a limited area in southeastern Texas (Fig. 20). Its range is separated by a gap of several hundred miles from that of the related species *T. fallax*. The *measured material* comes from the following localities: *Texas*: Anderson, Houston, An-

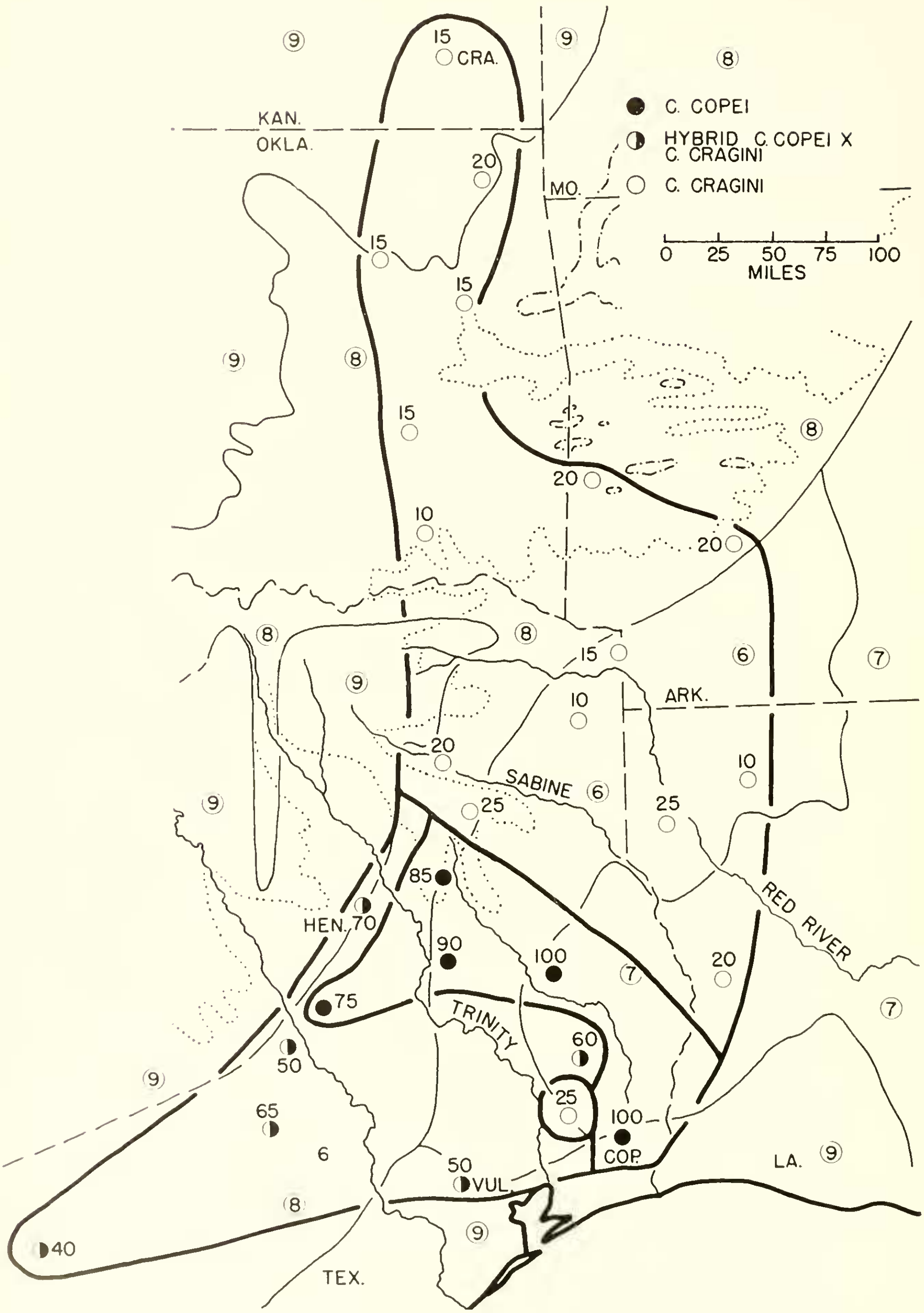

Figure 20. Distribution and the geographic variation of the character index in *Triodopsis copei*. Thick, solid line surrounds the range of c. *cragini*, c. *copei*, and hybrid c. *cragini* × c. *copei*. COP, type locality of c. *copei*; CRA, c. *cragini*; HEN, *henriettae*; VUL, *vultuosa*; the latter two forms are considered hybrid c. *cragini* × c. *copei*. Numbers without a circle are mean values of samples in character index; samples of c. *cragini* range from 5–35, hybrid, 40–70, c. *copei*, 75–100. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

gelina, and Jefferson counties (ANSP); Robertson County (MCZ). A total of 5 samples, 2–7 specimens each, 16 specimens altogether.

Ecology. Triodopsis c. copei occurs predominantly in oak-pine and southeastern evergreen forests, but it also penetrates the oak-hickory forests and grasslands (Fig. 20). It ranges from roughly 100 feet to about 500 feet elevation. This is very remarkable, in view of the fact that it has the large lip teeth and parietal lamella of a "mountain" snail. I cannot offer any satisfactory explanation for this anomaly.

Systematics. Triodopsis c. copei was originally described as a full species *or* a variety of *vultuosa.* Subsequently, it was ranked as either a variety or a subspecies of *vultuosa.* The type population of *vultuosa* is, however, a hybrid between *copei* and *cragini*; the name *vultuosa*, therefore, should not be used. The oldest available name for the species thus becomes *copei*, and the former *vultuosa copei* becomes *c. copei.*

Triodopsis copei cragini Call
Plate III: 16–18

Triodopsis cragini Call, 1886, Bull. Washburn College Lab. Nat. Hist. 1: 202, fig. 5. Banks of Chetopa Creek, Thayer, Neosho County, Kansas. Type MCZ 3123; paratypes MCZ 3124.

Definition. Triodopsis c. cragini is the former *T. cragini.* It comprises those populations of the species with mean values of 0–30 in character index. The method of computing character index is shown in Table X (p. 199).

Description. Shell width 7.7–10.8 mm; height 3.7–6.7 mm, height to width ratio 0.48–0.67; umbilicus 1.1–2.0 mm, umbilicus to width ratio 0.13–0.19; number of whorls 4.3–5.5, whorl to width ratio 0.47–0.60; embryonic whorls 1.4–1.5, feebly striated below suture, smooth elsewhere; striation becoming more pronounced on later whorls, 4–5 striae per millimeter on last whorl; aperture squarish to rounded; lip swelling moderately thick; lip teeth moderately large and angular; fulcrum usually absent, small if present; projection on face of lower lip small or absent.

Differential diagnosis. Triodopsis c. cragini is easy to distinguish from *T. c. copei* because its shell is smaller and more tightly coiled, and its armature is weaker. It is more difficult to distinguish from *T. f. obsoleta* or *f. alabamensis.* It is differentiated from the former by its square to rounded aperture and higher whorl to width ratio; from the latter it differs in having fewer whorls and a broader upper lip tooth. If we recall that *T. c. copei* resembles *T. f. fallax*, a parallelism between *T. copei* and *T. fallax* becomes evident. Both have evolved a large subspecies with heavy armature, and one or two small subspecies with light armature.

Distribution. Triodopsis c. cragini occurs in a narrow band running from Kansas to Texas and Louisiana, avoiding the Ozark Mountains (Fig. 20). In Texas it is contiguous with *T. c. copei.*

The *measured material* comes from the following localities: *Kansas*: Neosho County (MCZ). *Oklahoma*: Craig, Tulsa, Muskogee, Pittsburgh, and Pushmataha counties (ANSP). *Arkansas*: Polk, Clark, and Miller counties (ANSP). *Louisiana*: Bienville and Vernon counties (MCZ); De Soto County (ANSP). *Texas*: Cass and Wood counties (ANSP); Smith and Hardin counties (MCZ). A total of 16 samples, 2–12 specimens each, 83 specimens altogether.

The record from Muskogee County (ANSP 4718, Brown Collection) may be erroneous. These specimens have a much smaller and flatter shell than any other specimen of *c. cragini* seen. They look much like hybrid specimens between *T. f. alabamensis* and *f. fallax* or *f. obsoleta* from Alabama. Also, there is a Muscogee County in the neighboring state of Georgia. Only two specimens are available, however, which does not permit a certain identification. For this reason I tentatively included this sample in *c. cragini.*

Ecology. *Triodopsis c. cragini* inhabits oak-hickory, oak-pine, and southeastern evergreen forests seemingly without any preference (Fig. 20). A few localities fall in the grasslands. It is possible, however, that these localities also lie in small patches of woods that do not show up on the large scale map used here. *Triodopsis c. cragini* is found between about 100 and 1000 feet elevation. It is remarkable that it is found at higher elevations than *c. copei* because *T. c. copei* has the appearance of a mountain snail, whereas *c. cragini* does not. No explanation is known for this "reversed" distribution (p. 239).

Systematics. *Triodopsis c. cragini* was described as a full species. Subsequently, it was considered either a variety of *vultuosa* (Singley, 1893), or a synonym of *copei* (Binney, 1890). Finally, its specific status was restored (Pilsbry, 1901, 1940), on the grounds that it differs from *vultuosa* by its smaller size, lack of fulcrum, and lack of the projection on the lower lip, and because Pilsbry believed there was no intergradation between them. As shown below, however, intergradation does occur. The specific status of *cragini* is therefore not warranted; correctly, we should consider it a subspecies conspecific with *copei.* Thus the name used in this paper: *T. copei cragini.*

Hybrid populations between *Triodopsis c. copei* and *c. cragini*
Plate III: 19

Some populations are intermediate between *T. c. copei* and *c. cragini* in morphological characters. This is expressed by their mean values in character index, which vary between 40 and 70. (The mean values of *c. cragini* range from 5 to 35, those of *c. copei* from 75 to 100.)

Such populations are known from the following localities: *Texas*: Freestone, Milan, Lee, Bexar, and Harrison counties (ANSP); Tyler County (MCZ). A total of 6 samples, 2–21 specimens each, 55 specimens altogether. The localities lie mainly in forested area, between 100 and 500 feet elevation (Fig. 20). However, one of the non-measured samples comes from "fields along top of hill . . . near entrance of ship channel into Galveston Bay" (ANSP 187-087).

The variation in character index of the intermediate populations is about normal, except for the population from Freestone County, which has much wider variation than any other sample of the species. On this basis, the former samples appear to be primary intergrades, the latter one a secondary intergrade or hybrid. It seems unlikely, however, that such a dual explanation could be true. It is more probable, for several reasons, that all intermediate populations are hybrids. First, there is great similarity between the distributional pattern of *T. copei* and the related species, *T. fallax.* In both species, the intermediate populations surround the southern subspecies (Figs. 17 and 20). Presumably, the evolutionary history of the two species is similar. Since the intergrades are hybrids in *fallax*, they may be hybrids in *copei*, also. Second, it is difficult to see how primary intergradation (variation) could explain the occurrence of intermediate populations around the range of *c. copei.* Immigration of *c. cragini* into the peripheral zone of the range of *c. copei*, and subsequent hybridization, explains this pattern better. Third, the existence of a sharp character gradient between *c. copei* and *c. cragini* also indicates secondary intergradation, as discussed in more detail below.

Not all intermediate populations show increased variation; this can be attributed to the fact that the populations available for comparison are too small. Character displacement cannot explain the existence and distribution of the intermediate populations, because *c. copei* and *c. cragini* do not overlap. Because they demonstrate the conspecificity of *copei* and *cragini*, these intermediate populations are of great significance.

The paratype specimen of *vultuosa*[1] closely approximates the hybrid specimens. The available specimens of another recognized form, *henriettae*,[2] also seem to be hybrids. It is proposed, therefore, that these names be no longer used, and that the name of the species under discussion be changed from *vultuosa* to *copei*.

Variation in Triodopsis copei. As *T. c. copei* and *c. cragini* are within the same spectrum of variation, it is justified to discuss them together in this section.

Aperture: Three grades of aperture can be distinguished according to the degree of development of the armature. These are referred to as aperture grades B, C, and D. Aperture grade A was omitted, because specimens comparable to grade A of *T. fallax* (very weak armature) do not occur in this species, and it is desirable to keep the nomenclature consistent. Specimens of aperture grade B have a moderately thick lip swelling, moderately large lip teeth and parietal lamella, and a narrow to moderately broad upper lip tooth (Plate III). The lip teeth and parietal lamella do not obstruct the aperture. The lip swelling in grade C is thicker, the lip teeth and parietal lamella larger, and the upper lip tooth broader than in grade B, and these structures obstruct the aperture to a degree. In grade D, the lip swelling is thick, the lip teeth and parietal lamella very large, and the upper lip tooth very broad; the aperture is greatly obstructed. Intergradation between the various grades occurs.

In a given population usually only one grade is found, but in some cases B mixes with C, or C with D. Populations made up solely of grade B specimens are classified as *c. cragini*, B + C populations as *c. cragini* or hybrid, C as hybrid, C + D as hybrid or *c. copei*, and D populations as *c. copei*. The final decision in the case of the B + C and C + D populations is based on other characters.

Aperture grade B occurs predominantly in the northern and eastern parts of the range, D in the center of the southern part of the range, and C around the latter. This, of course, corresponds to the distribution of the two subspecies and the hybrids.

Fulcrum: This may be large, small, or absent. The absence of a fulcrum is a characteristic of specimens of aperture grade B, a small fulcrum of grade C, and a large fulcrum of D. Occasionally, however, a small fulcrum may occur in grade B, and a large one or none in C.

Measured characters: Height and umbilicus are correlated with width (size). Whorl number is also correlated with width within each subspecies, although *c. cragini*, of smaller dimensions, has relatively more whorls than *c. copei*. The measured characters are, to an extent, also correlated with aperture grades and the development of the fulcrum. Smallest and lowest are specimens of aperture grade B, larger and higher of grade C, etc. The geographic variation of the measured characters shows basically the same pattern as the character index.

Character index: Shell width (size), umbilicus, whorl to width ratio, aperture grade, and fulcrum grade were utilized in preparing the character index (Table X). The mean values of populations in character index are uniformly low in the northern and eastern parts of the range (Fig. 20). A high "plateau" of character index occurs in the southern-central region. Intermediate character index values surround the high plateau with the exception of the northeast; here the high values directly confront low ones, thus forming a very sharp character gradient.

This gradient runs from northwest to southwest, across eastern Texas, following

[1] *Helix vultuosa* Gould, 1848, Proc. Boston Soc. Nat. Hist. 3: 39. As type locality, Gould gave "Arkansas and Texas." The examined paratype, ANSP 187539, is most similar to specimens from Houston, Harris County, Texas. On this basis the type locality is here restricted to Houston.

[2] *Helix* (*Triodopsis*) *henriettae* Mazyck, 1877, Proc. Acad. Nat. Sci. Philadelphia, p. 297. "Eastern Texas." Type not seen.

no apparent physiographic barrier. The Sabine and Neches rivers, which run parallel with the gradient only a short distance away, scarcely qualify as barriers. It seems likely, therefore, that historical factors are responsible for the sharpness of the gradient. Presumably, the populations that presently confront each other developed their differences in isolation; their present contact is secondary.

Systematics. *T. copei* could be regarded either as conspecific with *T. fallax* or as a separate species. It is not known whether the two are reproductively isolated. Because *f. alabamensis* (which is morphologically less similar to *f. fallax* or *f. obsoleta* than are *c. copei* or *c. cragini*) can interbreed with *f. fallax* and *f. obsoleta*, it might be assumed that *c. copei* and *c. cragini* also can. Hence, we could consider *copei* and *fallax* conspecific. The method of estimating the potentiality of interbreeding has, however, repeatedly proved erroneous (p. 232). Also, both species have already split into several subspecies. I think, therefore, that *copei* and *fallax* should not be combined in one species.

Evolution. On morphological grounds it seems certain that *T. copei* developed from the same stock as *T. fallax*. The subsequent evolution of the two species proceeded along parallel lines. Both have produced a "mountain" and one or two "lowland" subspecies. The situation in *T. copei* is complicated, however, by the fact that the "mountain" subspecies only looks that way, and in fact occurs in lower areas than the supposed lowland subspecies does. We cannot tell, therefore, what forces can possibly be held responsible for the development of the two subspecies.

Summary. (1) *Triodopsis copei* corresponds to the *vultuosa-cragini* complex of contemporary authors. It is divided into two subspecies: *c. copei* and *c. cragini*. The first corresponds to the former *vultuosa copei*, the second to *cragini*. The two subspecies intergrade; this intergradation is presumably secondary (hybridization). Two of the hybrid populations, *T. v. vultuosa* and *T. v. henriettae*, are considered separate subspecies by contemporary workers.

(2) The range of *T. c. copei* is contiguous with that of *c. cragini*; the hybrid populations surround the range of the former. This pattern is not correlated with any physiographic feature.

(3) *Triodopsis c. copei* occurs at low elevations. This is not in accordance with its heavy armature, which is typical of mountain species. *Triodopsis c. cragini* ascends to somewhat higher elevations.

(4) The geographic variation is irregular within each subspecies.

(5) On morphological grounds it can be assumed that *T. copei* evolved from the same ancestor as *T. fallax*, and developed along parallel evolutionary lines with that species.

Triodopsis soelneri (J. B. Henderson)

Polygyra soelneri J. B. Henderson, 1907, Nautilus 21: 13, pl. 3, figs. 1–2. Among cypress logs on the north shore of Lake Waccamaw, Columbus County, North Carolina. Type ANSP 94682.

Definition. *Triodopsis soelneri* is recognized here as defined by its author.

Description. The description is based partly on Henderson's original description (1907), on Pilsbry's (1940) and Hubricht's (1950a) data, and partly on my own measurements.

Shell width 10.0–11.0 mm; height 6.3–7.2 mm; umbilicus very narrow, partially covered by reflection of lower lip; number of whorls 5.5; embryonic whorls 1.5, finely striated below suture, smooth otherwise, subsequent whorls with strong striae and, in the intervals of striae, with papillae; papillae scarce except in umbilical region where numerous; aperture oblique-oval; lip swelling bladelike, but becoming obsolete near junction of lower lip with shell; upper lip tooth small or absent, lower lip tooth absent; parietal lamella long and slightly bent.

Differential diagnosis. The bladelike lip swelling which usually does not bear any tooth, the partially covered umbilicus, the small dimensions of the shell, and the lack of complex sculpture readily distinguish *soelneri* from the species of the *T. obstricta* group, to which it shows superficial similarities.

Distribution. In addition to the type locality, Lake Waccamaw, Columbus County, North Carolina, Hubricht (1950a, 1953) has reported *T. soelneri* from Bladen, Brunswick, and Jones counties, all in North Carolina.

Ecology. The type locality was a cedar swamp on the northern shore of Lake Waccamaw. As Hubricht reports, this area has been drained and is being built on; he predicts that the type population will soon be exterminated. A second type of habitat in which *soelneri* is found is pine woods (Hubricht, 1953). The pine woods specimens, according to Hubricht, are smaller and have "a small but distinct denticle on the outer [upper] lip."

T. soelneri has been found coexisting with *T. hopetonensis* and *T. messana* (considered hybrids between *f. fallax*, *f. obsoleta*, and *f. alabamensis* in this paper [p. 198]).

The range of variation of *Triodopsis soelneri* is very narrow, probably because of its limited area of distribution and small population size.

Systematics. As Pilsbry pointed out (1940: 815), *T. soelneri* "is a somewhat isolated snail, as near to *T. hopetonensis* as to any of the fully toothed species. This estimate of its affinities is confirmed by the structure of the penis, the fleshy body within the upper cavity being similar to that of *hopetonensis* but much shorter. . . ."

Summary. Triodopsis soelneri is an isolated species within the *fallax* complex. It occurs in a restricted area. Its range of variation is narrow.

Subgenus *XOLOTREMA*

Xolotrema Rafinesque, 1819, J. Phys. Chim. Hist. Nat., 88; *non Xolotrema* Rafinesque, 1831.

Type. Triodopsis o. denotata, designated by Pilsbry (1940: 823).

The shell is usually larger than in the subgenus *Triodopsis*, imperforate, and with a characteristic sculpture. The aperture has a long, bladelike lamella in the lower lip instead of a lip tooth.

The subgenus contains only one species complex, *obstricta*.

Rafinesque did not designate a type species for *Xolotrema*. Furthermore, he used the term in two different ways, in 1819 and 1831. Pilsbry (1940: 823) clarified the meaning of the term *Xolotrema*, and designated *T. notata* (in this paper called *T. obstricta denotata*) as type species. Pilsbry's reasoning was that *T. o. denotata*, as well as all the other forms included in the *obstricta* complex, is recognizable from Rafinesque's 1819 description of *Xolotrema* as belonging to the genus, and is thus available as the type species. Rafinesque's 1831 description of *Xolotrema* refers to the *Mesodon inflectus* group.

THE *OBSTRICTA* COMPLEX

This complex contains two well-distinguished species: *Triodopsis obstricta*, with subspecies *o. obstricta* and *o. denotata*, and *T. fosteri*, with subspecies *f. fosteri* and *f. hubrichti*. The two subspecies of *T. obstricta* hybridize. The separation of two subspecies of *T. fosteri* may not be warranted.

Triodopsis obstricta (Say)
Triodopsis obstricta obstricta (Say)
Plate IV: 5, 6

Helix obstricta Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 145. "Inhabits Ohio." There is a specimen in the ANSP, 11271, labelled as "Probably the type," from Ohio. This is probably in error, however, since *obstricta* seems not to occur in Ohio (see systematics). I therefore restrict the type locality to Murfreesboro, Rutherford County, Tennessee, which falls within the range of the subspecies.

Carocolla helicoides Lea, 1834, Trans. Amer. Philos. Soc. 4: 103, pl. XV, fig. 34a–c. Near Nashville, Davidson County, Tennessee. Type not seen.

Definition. Triodopsis o. obstricta corresponds to *T. obstricta* of Pilsbry (1940),

TABLE XI

CHART FOR COMPUTING CHARACTER INDEX IN *TRIODOPSIS OBSTRICTA*. METHOD OF CALCULATION: A SPECIMEN WITH SCULPTURE D AND ANGULARITY TYPE 4 IS SCORED 55 + 45 = 100, THE AVAILABLE MAXIMUM SCORE.

Score	Sculpture	Angularity	
0	A	1	*o. denotata*
5	A′		↑
10	B		
15		2	
20			
25			
30	C	3	
35			
40			
45		4	
50	D′		↓
55	D		*o. obstricta*

less *T. o. occidentalis*. It contains those populations of the species which have mean values of 80–100 in character index. The method of computing character index is shown in Table XI.

Description. Shell width 19.7–25.9 mm; height 9.6–12.6 mm, height to width ratio 0.41–0.56; umbilicus covered or nearly so; number of whorls 5.2–5.8, whorl to width ratio 0.22–0.27; embryonic whorls 1.4–1.5, finely striated; subsequent whorls with stronger striation; last whorl with very strong striae on upper side, weak striae on under side; intervals between striae or ribs with closely set, fine wrinkles running in a transverse, oblique, or spiral direction; transverse wrinkles often arranged in spiral rows; last whorl with prominent keel along its periphery; aperture oval; lip swelling thick, with a flat or concave face; upper lip tooth well developed, flat; lower lip tooth replaced by a long, bladelike lamella, running to columellar wall; parietal lamella long, low, slightly curved, pointing above upper lip tooth.

Distribution. *Triodopsis o. obstricta* is confined to the Cumberland Mountains of eastern Tennessee and adjoining Alabama (Fig. 21). The *measured material* comes from the following localities: *Tennessee*: Pickett, Overton, Davidson, Rutherford, Grundy, Franklin, and Maury counties (MCZ). *Alabama*: Jackson (2 samples) and Madison counties (2 samples) (MCZ). A total of 11 samples, 2–7 specimens each, 41 specimens altogether.

Ecology. The range of *T. o. obstricta* is mountainous, but never exceeds 1500 feet elevation. It is covered by mixed and western mesophytic forests (Fig. 21). Its eastern boundary runs parallel with the 1500-foot contour line, but elsewhere the boundaries do not correspond to physiographic features.

Systematics. Say gave "Ohio" as the type locality of *T. o. obstricta*. This was probably in error, however, since *o. obstricta* is not known from Ohio (except Taft's record, 1961, from Pickaway County, which is probably a hybrid between *o. obstricta* and *o. denotata*). Say's specimen agrees well with those from Tennessee. On this basis, I restrict the type locality to Murfreesboro, Rutherford County, Tennessee. If this interpretation is correct, *C. helicoides* must be considered synonymous with *o. obstricta*.

A population from the Ozark Mountains has been described by Pilsbry and Ferriss (1907) as *T. o. occidentalis*. Under the microscope, however, these shells show the papillate sculpture of *Mesodon sargentianus*, and therefore must be placed with that species.

Triodopsis obstricta denotata (Férussac)
Plate IV: 1, 4, 12

Helix palliata Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 152. "Illinois." Non *Helix palliata* Hartmann, 1807. Type ANSP 11256.

Helix denotata Férussac, 1821, Tableaux Systematiques des Animaux Mollusques, p. 34, no. 102 (*nomen nudum*). *H. denotata* is cited as a synonym of *palliata* in Férussac and Deshayes: Histoire Naturelle des Mollusques Terrestres et Fluviatiles, 1820–1851, p. 144, pl. 49a, fig. 5.

Helix notata "Fér." Deshayes, 1832, Encyclopédie Methodique Histoire Naturelle des Vers, par Bruguière et de Lamarck, continuée par G. P. Deshayes, Vol. 2, part C-MYT, p. 224. "Kentucky." Type not seen.

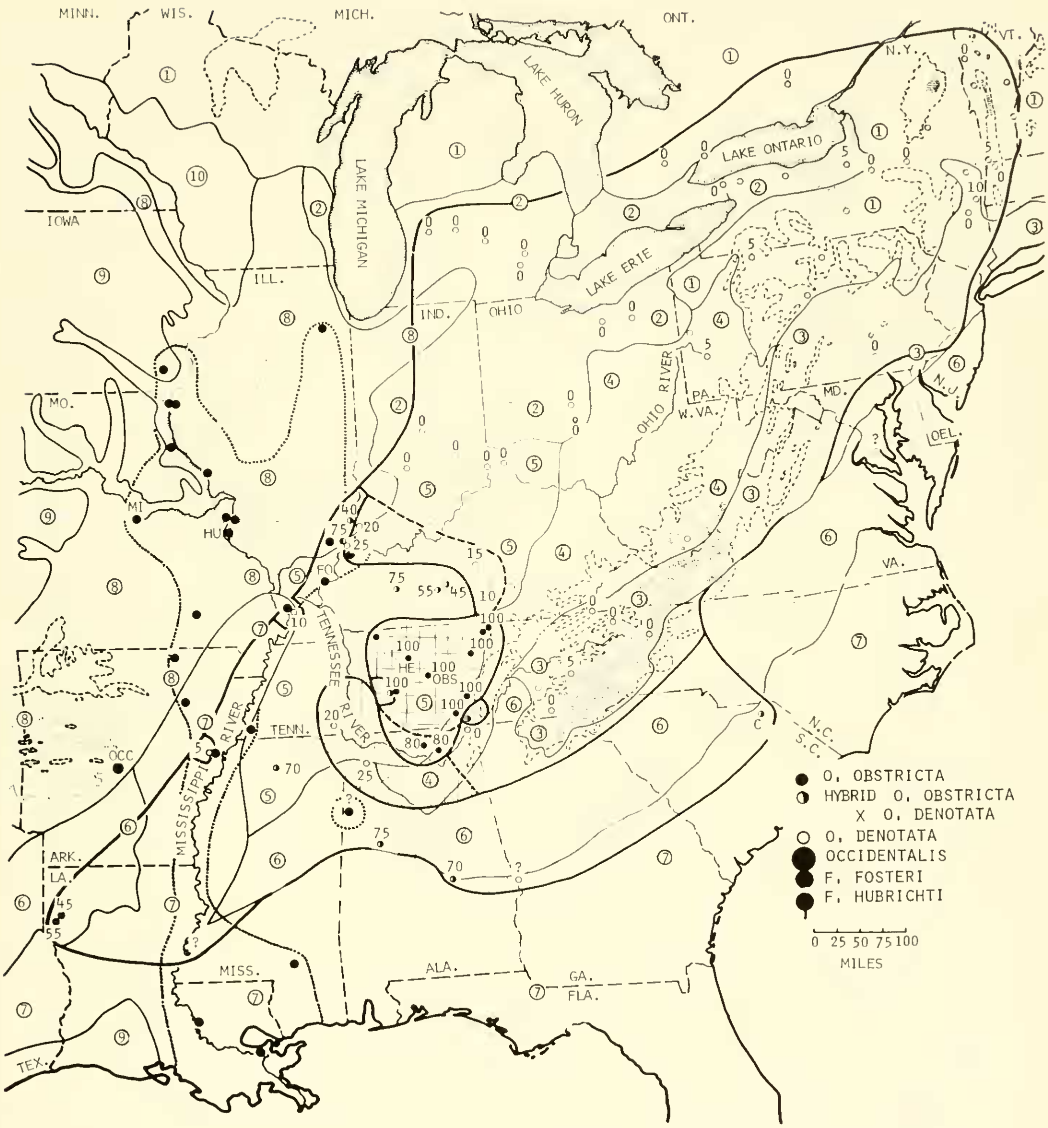

Figure 21. Distribution of *Triodopsis obstrica* and *fosteri*, and the geographic variation of the character index in *obstricta*. Thick, solid line surrounds the range of o. *obstricta*, o. *denotata*, and hybrids between the two subspecies; thick, dashed line, those peripheral areas of the range where limited interbreeding took place; dotted line surrounds the range of *fosteri*. Question mark beside a symbol means uncertain locality record. C., type locality of *caroliniensis*, considered hybrid o. *obstricta* × o. *denotata*; HE., *helicoides*, considered synonymous with o. *obstricta*; OBS., o. *obstricta*; OCC., *occidentalis*, considered synonymous with *Mesodon sargentianus*; FO., f. *fosteri*; HU., f. *hubrichti*; MI., *missouriensis*, considered synonymous with f. *fosteri*. Numbers without a circle are mean values of samples in character index; the samples of o. *denotata* range from 0 to 25, hybrid 40–75, o. *obstricta*, 80–100. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Definition. *Triodopsis o. denotata* corresponds to *T. notata* of Pilsbry (1940: 824), who combined *notata*, *denotata*, and *palliata*. It combines those populations of the species which have mean values of 0–25 in character index (Table XI).

Description. Shell width 17.0–25.9 mm; height 8.5–12.9 mm, height to width ratio 0.42–0.57; umbilicus completely or partially covered; number of whorls 4.8–5.8, whorl to width ratio 0.21–0.30; embryonic whorls 1.4–1.5, striated; striation becoming more pronounced toward aperture; intervals between striae with triangular scales; space between scales with fine, transverse wrinkles; last whorl angular or obtusely angular at its periphery; aperture oval; lip swelling well developed, flat; upper lip tooth also well developed, flat; lower lip tooth replaced by a long, bladelike lamella; parietal lamella long, low, slightly curving, pointing above upper lip tooth.

Differential diagnosis. *Triodopsis o. denotata* is readily distinguishable from *T. o. obstricta* because of its scaly sculpture and weaker striation, and because it lacks a keel on the periphery of the last whorl.

Distribution. *Triodopsis o. denotata* ranges from Michigan and New Hampshire in the north to Alabama and Georgia in the south. Isolated populations also occur outside of this range, in Tennessee, Arkansas, and Louisiana (Fig. 21).

The *measured material* (all MCZ) comes from the following localities: *Ontario*: Hastings, Wellington, York, and Lincoln counties. *Vermont*: Chittenden and Bennington counties. *Massachusetts*: Berkshire County. *New York*: Dutchess, Columbia, Herkimer, Madison, and Onondaga counties. *Michigan*: Kent, Oakland, Washtenaw, Ingham, and Ionia counties. *Pennsylvania*: Lancaster, McKean, and Allegheny counties. *Ohio*: Summit, Lorain, Franklin, Pickaway, and Hamilton counties. *Indiana*: Marion, Dearborn, Decatur, Monroe, Gibson, and Posey counties. *Maryland*: Plummer Island (?county). *Virginia*: Lee County. *North Carolina*: Avery and Cherokee counties. *Kentucky*: Casey and Marion counties. *Tennessee*: Sullivan, Sevier, and Hardin counties. *Alabama*: Jackson and Franklin counties. A total of 42 samples, 2–24 specimens each, 197 specimens altogether.

Ecology. *Triodopsis o. denotata* occurs in various kinds of deciduous forests, predominantly between 500 and 1500 feet elevation (Fig. 21). Only a few localities occur below 500 feet. These populations were perhaps carried down by the streams, as is the case in *T. j. juxtidens*, *T. fraudulenta*, and *T. m. mullani*. We found *T. o. denotata* in greater abundance on the banks of creeks than high up on the hills. On the hills it coexists with *T. tridentata*; it does not seem to coexist, however, with the related species *T. fosteri*.

Systematics. Under *T. notata*, Pilsbry combined *palliata*, *denotata*, and *notata*. The first name is a homonym, and therefore cannot be used. *Helix denotata* Férussac, 1821, was published before *notata* Férussac, 1832 (see synonymy), but without a description. On this basis Pilsbry (1940: 824) called the taxon *notata*. But, as Pilsbry himself pointed out (1948: 1100), *denotata* was cited by Férussac in 1823 as equal to *palliata*; thus *denotata* is the valid name.

Some authors treat *T. o. denotata* as a full species, neglecting the intergradation that exists between this form and *o. obstricta*. I believe that because intergradation (hybridization) occurs, the two forms must be considered conspecific.

Hybrid populations between *Triodopsis o. obstricta* and *o. denotata*
Plate IV: 2, 3

Some populations are morphologically intermediate between *T. o. obstricta* and *o. denotata*; the mean values of these populations in character index range from 40–75, of *o. obstricta* from 80–100, of *o. denotata*, 0–25. Intermediate populations are known from an almost complete ring around the range of *o. obstricta* (Fig. 21). The *mea-*

sured material (all MCZ) comes from the following localities: *Indiana*: Posey County. *Illinois*: Wabash County. *Kentucky*: Hart, Edmonson, and Ohio counties. *Alabama*: Elmore and Tuscaloosa counties. *Mississippi*: Lafayette County. *Louisiana*: De Soto County (2 samples). A total of 10 samples, 2–5 specimens each, 28 specimens altogether.

The intermediate populations appear more variable than the populations of *T. o. obstricta* or *o. denotata*, so that they may be considered hybrids between the two subspecies. This interpretation is consistent with the fact that the intermediate populations are found in a zone that lies between the two subspecies, and on the periphery of the range of *o. obstricta* (see also p. 237).

One of the hybrid populations, from South Carolina, has been described as *Triodopsis caroliniensis*.[1] This name is placed, according to the rules, in the synonymy.

The hybrid populations show that *T. o. obstricta* and *o. denotata* are not isolated reproductively, and can thus be combined in one species.

Variation in Triodopsis obstricta. The variation of several characters is continuous through the two subspecies. It is, therefore, best to discuss the variation of both subspecies together.

Sculpture: Four types can be distinguished, referred to as A, B, C, and D. Shells of type A are moderately striated. In the spaces between the striae, large, triangular scales are found, arranged in oblique rows. From the base of each scale several short and thick wrinkles radiate out, dividing the shell surface into small polygons. The latter, in turn, are covered by very fine wrinkles, running in a transverse direction (Pl. IV, fig. 12). Type B resembles A closely, but the thick wrinkles may fuse to long, jagged lines. Type C is a mixture of A and D, and therefore will be described after D. Type D has very strong striae, almost like ribs. The fine sculpture consists of short wrinkles or lines, running in transverse, oblique, or spiral directions. When transverse, the fine wrinkles may be arranged in spiral rows. In type C, the polygonal sculpture and the scales of A occur together with the wrinkled sculpture of D; e.g., the upper side of the last whorl may be covered by short lines, the under side by polygons and very fine transverse wrinkles. Another type of sculpture also was considered C. This is a network of relatively thick, long wrinkles, in the meshes of which are visible short, transverse wrinkles. The striae in both types of C are as strong as in D.

Type A is characteristic of *T. o. denotata*, D of *o. obstricta*. Type B and type C occur in the hybrids and occasionally in some non-hybrid specimens. Type A is, accordingly, common in the northern half of the range, D in eastern Tennessee, B and C northwest, west, and south of the area of D.

Angularity of the last whorl: Four types can be distinguished, referred to as 1, 2, 3, and 4 (Plate IV). In 1, the periphery of the last whorl is rounded or bluntly angular, in 2 it is angular, in 3 sharply angular, without a keel, and in 4 sharply angular, with a keel. Type 1 is characteristic of *o. denotata*, 2 and 3 of the intermediates, and 4 of *o. obstricta*. Type 2 also occurs sporadically in otherwise "pure" populations of *o. denotata*.

Measured characters: Shell width is correlated with height and number of whorls. All measured characters show irregular geographic variation.

Character index: This was prepared by assigning numerical values to the various types of sculpture and angularity of the last whorl, and summing up these values. Thus a specimen of sculpture type A and angularity type 1 was scored $0 + 0 = 0$, etc. (Table XI).

The mean values of populations in char-

[1] *Triodopsis caroliniensis* Lea, 1834, Trans. Amer. Philos. Soc. 4: 102, pl. 15, figs. 33a–c. Cheraw, Chesterfield County, South Carolina. Type ANSP 11267.

acter index range from 0 to 100. Low values, between 0 and 25, correspond to *o. denotata*, high values, between 80 and 100, to *o. obstricta*, intermediate values, between 40 and 75, to hybrids. Populations with extremely low values are found in the northern and eastern parts of the range (Fig. 21). Populations with high values of 80–100 occur in eastern Tennessee, those with intermediate values northwest, west, and south of the latter. The change from low to high values is generally abrupt, but particularly so on the eastern side of the area of high values, where populations with mean values of 100 confront others with values of 0.

As to the origin of this pattern, we may put forward the following hypothesis. The differences between the two subspecies developed while they were isolated from one another. The intergradation between them is secondary, due to hybridization. The northern subspecies, *o. denotata*, invaded the periphery of the range of the southern subspecies, *o. obstricta*, and in places made quite deep inroads in it. In the invaded areas, hybridization is going on. In only one place did *o. denotata* not invade: in the east, where the Cumberland Mountains guard the eastern border of *o. obstricta*. Here hybrids are missing, and the "transition" from *o. denotata* to *o. obstricta* is sharp.

It seems unlikely that the above pattern of variation could be explained by primary intergradation. Should that be the case, we would expect the variation to reflect the physiographic pattern of the area, which it does not. Character displacement is almost certainly not involved, either. In character displacement, the most distinct populations should occur in the zone of overlap, the least distinct, outside. In this case, however, the distribution is just the reverse.

Summary. (1) *Triodopsis obstricta* is divided into two subspecies: *o. obstricta* and *o. denotata*. The two subspecies intergrade with each other, and the intergradation is presumably secondary. One of the intergrading (hybrid) populations has been mistakenly described as a separate species, *T. caroliniensis*. The currently recognized subspecies *T. o. occidentalis* is to be placed with *Mesodon sargentianus* as a synonym.

(2) *Triodopsis o. denotata* has a northern distribution, *o. obstricta* a southern one. The hybrid populations form an almost complete ring around the southern subspecies.

(3) *Triodopsis o. denotata* possibly shows ecological exclusion with *T. fosteri*.

(4) Both subspecies show irregular geographic variation.

Triodopsis fosteri (F. C. Baker)
Triodopsis fosteri fosteri (F. C. Baker)
Plate IV: 7–9

Polygyra appressa var. *fosteri* F. C. Baker, 1932, Nautilus 46: 48. Three miles northwest of Elizabethtown, in valley of Big Creek, Hardin County, Illinois. Paratypes ANSP 157437 and MCZ 92462.

Triodopsis fosteri forma *missouriensis* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 833, fig. 487i,j. Jefferson City, Cole County, Missouri. Type ANSP 11289; paratypes ANSP 168631.

Definition. Triodopsis f. fosteri includes the former *T. f. fosteri* and *f. missouriensis.*

Description. Shell width 13.8–22.0 mm; height 6.9–11.0 mm, height to width ratio 0.43–0.58; imperforate; number of whorls 4.6–5.5, whorl to width ratio 0.25–0.35; whorls flat, periphery of last whorl slightly angular; embryonic whorls 1.4–1.5, striated; striation becoming coarser toward aperture; 3 striae per millimeter on last whorl; space between striae with fine spiral threads; very short and very fine transverse wrinkles between spiral threads; details visible only on a fresh shell, under magnification of 25 × or higher; aperture oval; upper lip tooth small or lacking; lamella replacing lower lip tooth also small or lacking; parietal lamella moderately or well developed.

Differential diagnosis. Triodopsis f. fosteri is easily separated from *T. o. obstricta* and *o. denotata* by its smaller size, characteristic sculpture, tighter coiling and weaker dentition. It is very similar, however, to *Mesodon appressus*; in fact, it was originally described as a subspecies of that form. The microscopic sculpture safely separates them, however; *Mesodon appressus* has regularly arranged papillae, or the shell is almost smooth. *Triodopsis f. fosteri*, on the other hand, has spiral threads and transverse wrinkles as described above. In addition, its shell is less flat than that of *appressus*.

Distribution. Triodopsis f. fosteri ranges from Iowa to Indiana in the east, and to Louisiana and Alabama in the south (Fig. 21). It was introduced in Burlington, New Jersey, in the 1860s by W. G. Binney. It established a thriving colony there. The Louisiana sample is actually labelled as Baton Rouge, Florida. I changed the state to Louisiana, because there is no Baton Rouge in Florida, and *f. fosteri* does not occur in that state.

The *measured material*, all MCZ, comes from the following localities: *Iowa*: Henry, Des Moines, and Lee counties. *Illinois*: Will, Hancock, Calhoun, St. Clair, Monroe, White, and Hardin counties. *Missouri*: Marion, St. Louis, and Carter counties. *Kentucky*: Ballard County. *Tennessee*: Shelby County. *Arkansas*: Sharp, Jackson, and Lee counties. *Alabama*: Lamar County. *Louisiana*: Orleans and East Baton Rouge counties. A total of 23 samples, 2–12 specimens each, 116 specimens altogether.

Ecology. Triodopsis f. fosteri is essentially confined to the Mississippi Valley (Fig. 21). It is seldom found over 500 feet elevation. Its range is covered by southeastern evergreen forests, on the alluvial plane of the Mississippi, or by oak-hickory forests, farther north. But it also invades the periphery of the grasslands and the western mesophytic forests.

In the Mississippi Valley, at Valmeyer, Monroe County, Illinois, we found *T. f. fosteri* living in great abundance on and at the foot of limestone bluffs that border the flood plains. We did not find any *T. o. denotata*, a related species that also occurs in the region, coexisting with it. This seems to indicate that the two species are ecologically exclusive of each other, but one observation is not sufficient to establish this conclusion definitely.

Variation. Sculpture: In three shells, deeply incised, spiral grooves replace the spiral threads in a part of the last whorl. This type of sculpture is probably the result of an injury to the shell, or, more accurately, to the mantle edge that produces the shell. In these three cases observed, the initial whorls bore normal sculpture, and the deep grooves appeared after a scar. Only single specimens showed such deep grooves, never whole demes. Several species of the subgenera *Neohelix* and *Cryptomastix* also show this phenomenon (p. 225, Pl. V, fig. 11).

Measured characters: Width of shell is correlated with height and whorl number. All characters show irregular geographic variation.

Systematics. Triodopsis f. fosteri was originally described as a subspecies of *Mesodon appressus*. Anatomical studies revealed, however, that it belongs in the genus *Triodopsis*.

Triodopsis f. missouriensis of Illinois and Missouri is "small, rather smooth. . . . The parietal tooth is short and high. . . . The upper lip tooth is quite small, usually distinct, but sometimes disappearing. . . ." (Pilsbry, 1940: 833). None of these characters really differentiates *missouriensis* from "typical" *fosteri*, however. In size, *missouriensis* ranges from 14.3 to 15.8 mm, the typical form, 13.8–22.2 mm. Of the two specimens Pilsbry figured, one has a short parietal lamella, but the other has a long one. The former has an upper lip tooth, the latter lacks one. The range of *missouriensis* is peripheral to that of *f. fosteri*, but is not isolated from the latter. All in all, I cannot see any reason for separating *missouriensis* from *f. fosteri*. Therefore, I consider it synonymous with the latter.

Triodopsis fosteri hubrichti (F. C. Baker) Plate IV: 10, 11

Polygyra appressa var. *hubrichti* F. C. Baker, 1937, Nautilus 51: 23. Valmeyer, Monroe County, Illinois, in pink loess of Sangamon age. Paratypes ANSP 168631.

Definition. Triodopsis f. hubrichti is recognized here as proposed by its author.

Description and differential diagnosis. This subspecies was characterized by its author as follows: "Shell differing from typical *appressa* in its much greater size, more elevated spire, rounded aperture, and general gibbous form. The parietal lamella is long, curved, and extends to the umbilical region as in the typical form. Basal lower tooth of peristome usually well developed, but the upper denticle of race *fosteri* rarely developed. Sculpture of fine lines of growth. Diameter 25.5; height 14.5; Ap. [aperture] diam. 10.0; height 7.0 mm." Later, Baker writes (1937: 23), however, that "there is considerable variation in size among the 50 specimens of *hubrichti* from Valmeyer, about a dozen specimens ranging from 19 to 21 mm in diameter."

In contrast, Pilsbry states that "the race is distinguished only by its large size" (1940: 834). Having seen the type population, I agree with him completely.

Distribution and ecology. Triodopsis f. hubrichti has been found in pink loess of Sangamon age, at Valmeyer, Monroe County, Illinois. This is on the banks of the Mississippi River, where *f. fosteri* occurs today. It therefore appears possible that *f. hubrichti* occupied habitats similar to those occupied by *f. fosteri* today.

Systematics. Triodopsis f. hubrichti is very similar to *f. fosteri.* In addition, it is probably directly ancestral to the latter. On this basis, we could combine them in one taxon. But *f. hubrichti* is chronologically isolated from *f. fosteri*, and for this reason is accepted as a valid subspecies.

Summary. (1) *Triodopsis fosteri* is divided into two subspecies; *f. fosteri* and *f. hubrichti.* The former is a Recent form, the latter a fossil. *Triodopsis f. missouriensis* is a synonym of *f. fosteri.*

(2) *Triodopsis f. fosteri* is confined to the Mississippi Valley. It possibly shows habitat exclusion with *T. o. denotata. Triodopsis f. hubrichti* presumably occurred in similar habitats.

(3) The geographic variation is irregular.

Evolutionary relationships in the Triodopsis obstricta complex. Triodopsis obstricta and *T. fosteri* are certainly related, but we do not know anything about their evolutionary history. *Triodopsis o. obstricta* and *o. denotata* are assumed to have descended from a common ancestor. They were once isolated, and during isolation started to diverge. But recently they have re-established contact and started hybridizing; this may lead to their eventual merging. *Triodopsis f. hubrichti* lived during the Pleistocene epoch (Sangamon age), in the same geographical area and possibly in similar habitats as *f. fosteri.* We can assume that *f. hubrichti* developed into *f. fosteri* through slow transformation (phyletic speciation).

Subgenus *NEOHELIX*

Neohelix von Ihering, 1892, Zeitschr. Wiss. Zool. 54: 482.

Type. Helix albolabris Say, designated by Pilsbry, 1930, Proc. Acad. Nat. Sci. Philadelphia 82: 326.

This subgenus differs from *Xolotrema* only in having a larger shell and more capacious whorls, and in lacking an armature in the aperture. It thus could be easily lumped with *Xolotrema.* I retain the present system only because of the reasons stated before (p. 148).

The subgenus consists of one species complex: the *albolabris* complex.

The *albolabris* Complex

This complex contains four well-differentiated species: *albolabris, dentifera, multilineata*, and *divesta. Triodopsis albolabris* has three subspecies: *a. albolabris, a.*

alleni, and *a. major*; the three other species are monotypic.

Triodopsis albolabris (Say)
Triodopsis albolabris albolabris (Say)
Plate V: 3, 6, 11

Helix albolabris Say, 1817, Nicholson's Encyclopaedia, 1st American Edition, article "Conchology," species number 1, pl. 1, fig. 1. Neotype from Philadelphia, Pennsylvania, designated by Pilsbry, 1940: 837, fig. 849. Neotype ANSP 20199.

Mesodon albolabris var. *dentata* Tryon, 1867, Amer. J. Conch. 3: 39, pl. 7, fig. 6. Type not seen.

Helix albolabris var. *maritima* Pilsbry, 1890, Proc. Acad. Nat. Sci. Philadelphia 42: 283, 3 figs. Sand hills at Cape May, Cape May County, New Jersey. Not *Helix maritima* Draparnaud, 1805. Type not seen.

Polygyra albolabris var. *minor* Sterki, 1900, Ann. Rep. Ohio State Acad. Sci. 8: 31. "On the bank along the river," New Philadelphia, Tuscarawas County, Ohio. Type not seen.

Polygyra albolabris var. *goodrichi* C. H. Clapp, 1916, Ann. Carnegie Mus. 10: 539, pl. 32, figs. 16–18. Middle Sister Island, Essex County, Lake Erie, Ontario, Canada. Paratypes MCZ 139673.

Definition. Triodopsis a. albolabris is recognized here as defined by Pilsbry (1940). It contains those populations of the species which have mean values of 25–50 in character index. The method of computing character index is shown in Table XII. The subspecies slightly overlaps *T. a. alleni* in character index. The reason is explained in a later section.

Description. Shell width 20.2–35.6 mm; height 11.5–23.9 mm, height to width ratio 0.52–0.73; no umbilicus; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striation becoming more pronounced on subsequent whorls, about 2–3 striae per millimeter on last whorl; space between striae with a grid formed by intersecting spiral lines (40–50 per millimeter) and transverse wrinkles; grid delicate on younger whorls, becoming coarser toward aperture; deep spiral grooves on whorls built after an injury to shell; aperture round-oval; lip swelling from thin to very thick; lip teeth and parietal lamella usually absent; lower lip tooth replaced by a low, diffuse swelling; small parietal lamella occasionally present.

Distribution. Triodopsis a. albolabris ranges from Quebec to Michigan in the north, and to North Carolina and Mississippi in the south (Fig. 22). Its range is larger than that of any other taxon of *Triodopsis*.

The *measured material*, all MCZ, comes from the following localities: *Maine*: Aroostook, Penobscot, Oxford, Knox, and Cumberland counties. *Quebec*: Terrebone and Rouville counties. *Ontario*: Leeds, Hastings, Ontario, Peel, Wentworth, Essex, and Norfolk counties. *New Hampshire*: Carroll and Cheshire counties. *Vermont*: Orleans, Chittenden, and Windsor counties. *Massachusetts*: Middlesex, Plymouth, and Hampden counties. *Rhode Island*: Newport County. *Connecticut*: Middlesex and Fairfield counties. *New York*: Clinton, Washington, Columbia, Dutchess, Ulster, Herkimer, and Otsego counties. *Michigan*: Cheboygan, Alpena, Lelanau, Tuscola, Ionia, Washtenaw, and Kalamazoo counties. *New Jersey*: Morris County. *Pennsylvania*: Pike, Northampton, Sullivan, Clinton, McKean, Indiana, Philadelphia, Lancaster, Dauphin, Fulton, and Somerset counties. *Ohio*: Summit, Belmont, Lucas, Pickaway, Adams, and Hamilton counties. *Indiana*: La Porte, Bartholomew, and Dearborn counties. *Maryland*: Baltimore, Somerset, Prince Georges, and Alleghany counties. *Virginia*: York, Norfolk, Louisa, Prince Edward, Rockbridge, Roanoke, Wythe, and Lee counties. *West Virginia*: Jefferson, Grant, Randolph, Summers, and Raleigh counties. *North Carolina*: Tyrell, Craven, Columbus, Durham, Mitchell, Henderson, and Swain counties. *Kentucky*: Hart County. *Tennessee*: Polk County. A total of 86 samples, 1–21 specimens each, 468 specimens altogether.

Ecology. Triodopsis a. albolabris occurs in a variety of forest types, between sea level and 4000 feet elevation (Fig. 22; the latter record from Pilsbry, 1940: 836).

TABLE XII

CHART FOR COMPUTING CHARACTER INDEX FOR *TRIODOPSIS ALBOLABRIS*. METHOD OF CALCULATION: A SPECIMEN WITH A SHELL WIDTH OF 40.0 MM, A HEIGHT TO WIDTH RATIO OF 0.75, SCULPTURE C, AND LOWER LIP TOOTH GRADE 4 WAS SCORED (70 + 70 + 30 + 30)/2 = 100, THE AVAILABLE MAXIMUM SCORE.

SCORE	WIDTH IN MM	HEIGHT TO WIDTH RATIO	SCULPTURE	LOWER LIP TOOTH GRADE	
0	20.2–22.1	0.54–0.55	A	1	*a. alleni*
5	22.2–24.1	0.56–0.57			↑
10	24.2–25.3	0.58–0.59		2	
15	25.4–26.4	0.60	B		
20	26.5–27.6	0.61		3	
25	27.7–28.7	0.62			
30	28.8–29.9	0.63	C	4	*a. albolabris*
35	30.0–31.0	0.64			
40	31.1–32.2	0.65			
45	32.3–33.3	0.66			
50	33.4–34.5	0.67			
55	34.6–35.7	0.68			
60	35.8–37.7	0.69–0.70			↓
65	37.8–39.7	0.71–0.72			*a. major*
70	39.8–41.7	0.73–0.76			

According to collectors' rather sporadic remarks on the ecology, it occurs not only in wooded areas but also in thickets on sandy shores and in salt marshes. It has been found on offshore islands too. The great number of samples available indicates that the species is rather abundant in nature.

In the thickets growing on sandy beaches (both sea and fresh water) and "on the higher spots in salt marshes" (Pilsbry, 1940: 839) a characteristically small, high, and thin-shelled form is usually present. This appears to be an ecological form of polytopic distribution. This form was once called *T. a.* var. *maritima*, but recent authors consider it synonymous with *T. a. albolabris* (Pl. V, fig. 6). Another polytopic, ecological form is *T. a.* forma *goodrichi*, which has a pinkish shell. It is found on a few islands in Lake Erie, and on the shores of Lake Waccamaw, North Carolina, all presumably very moist places. This form also is considered synonymous with *T. a. albolabris*.

Variation. Aperture: The lip teeth are usually lacking. Rarely, however, a moderate to heavy swelling appears close to the columella, possibly replacing the lower tooth. A parietal lamella occurs sporadically in many populations.

Measured characters: Height of the shell is correlated with width; both characters show irregular geographic variation.

Systematics. The synonymy of *T. a. albolabris* has been summarized by Pilsbry (1940: 835), and is only recapitulated here. *Triodopsis a.* var. *maritima* and var. *goodrichi* are ecological forms, and var. *dentata* (Pl. V, fig. 2) is based on individual variation. *Polygyra a.* var. *minor* is a preoccupied name.

Triodopsis albolabris major (A. Binney)
Plate V: 9, 10

Helix major A. Binney, 1837, Boston J. Nat. Hist. 1: 473, pl. 12. "Georgia, Alabama, and Florida." Neotype selected by Pilsbry, 1940: 844, fig. 489 1, "Georgia," ANSP 11212.

Definition. Triodopsis a. major is recognized here as defined by Pilsbry (1940). It contains those populations of the species of which the mean character index values range between 65 and 95. The method of computing character index is shown in Table XII.

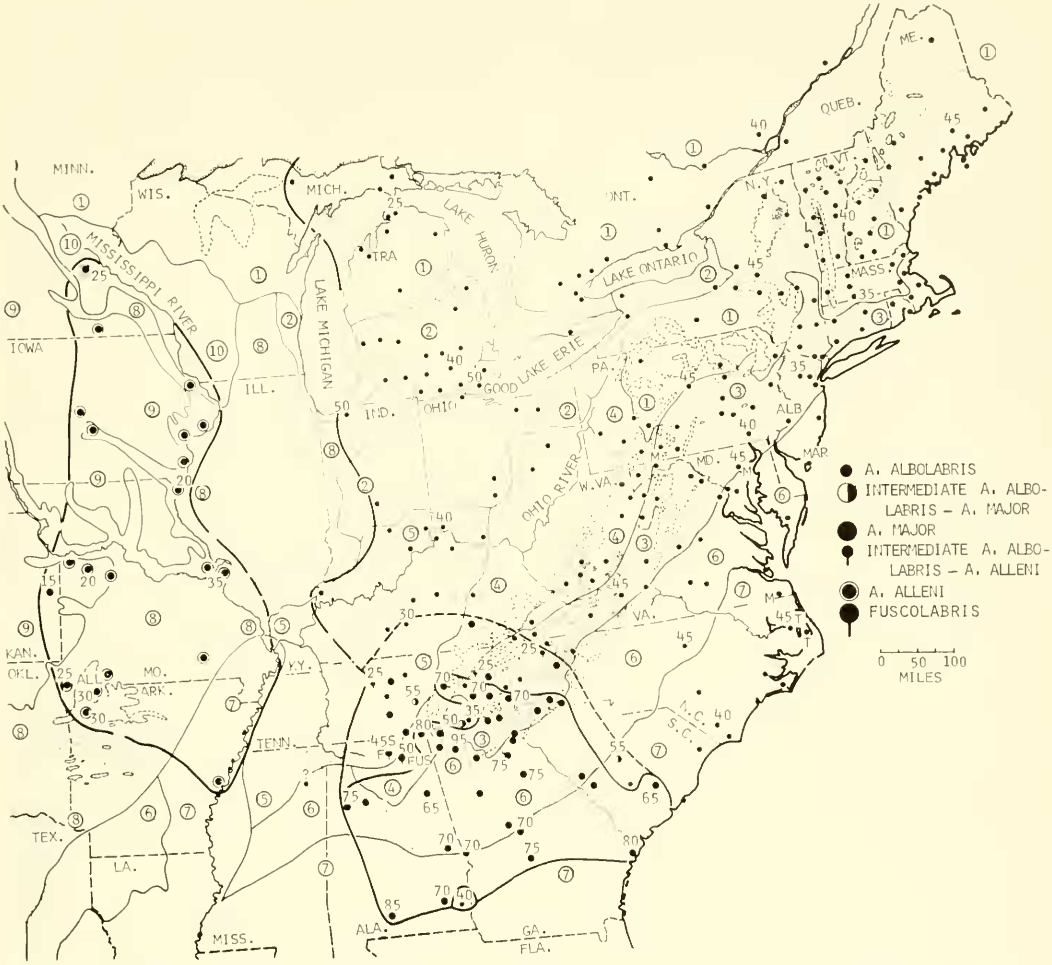

Figure 22. Distribution of *Triodopsis albolabris*. Thick, solid line surrounds the range of *a. albolabris*, *a. major* and *a. alleni*; thick, dashed line separates the zone of intergradation from the range of *a. albolabris*. F, occurrence of *fuscolabris*; M, *maritima*; T, *traversensis*; the latter two forms are considered synonymous with *a. albolabris*. ALB., type locality of *a. albolabris*; ALL., *a. alleni*; FUS., *fuscolabris*; GOOD., *goodrichi*, considered synonymous with *a. albolabris*; MAR., *maritima*; TRA., *traversensis*. Numbers without a circle are mean values of samples in character index; samples of *a. albolabris* range from 25 to 50; intermediate between *a. albolabris* and *a. major*, 50–55; *a. major*, 65–95; intermediate between *a. albolabris* and *a. alleni*, 25; *a. alleni*, 15–35; *fuscolabris*, considered intermediate between *a. alleni* and *a. major*, 45–50. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

Description and differential diagnosis. Shell larger, higher, and more globose than that of *a. albolabris*; width 27.1–41.7 mm; height 18.8–30.5 mm, height to width ratio 0.62–0.74. Sculpture same as in *a. albolabris*, perhaps a little coarser. Lip swelling usually very thick; the swelling replacing the lower lip tooth is present in about two-thirds of the specimens; parietal lamella absent. In *a. albolabris*, the lip swelling is usually thinner, and the lip swelling and the parietal lamella are present occasionally.

Distribution. Triodopsis a. major is confined to a small area from North Carolina to Alabama (Fig. 22). A narrow zone of intergradation separates its range from that of *T. a. albolabris.* The range roughly coincides with that of *T. f. alabamensis*, a not very closely related, congeneric species.

The *measured material*, all MCZ, comes from the following localities. *North Carolina*: Swain County. *South Carolina*: Berkeley County. *Tennessee*: Blount, Loudon, Cumberland, and Marion counties. *Georgia*: Whitefield, Hall, Clarke, Bibb, Chatham, Pulaski, and Muscogee counties. *Alabama*: Fayette, Calhoun, Lee, Barbour, Henry, and Conecuh counties. A total of 19 samples, 1–8 specimens each, 41 specimens altogether.

Ecology. Triodopsis a. major is common in oak-pine and southeastern evergreen forests, but also occurs in mixed and western mesophytic and oak-hickory forests. It ranges from sea level to over 3000 feet (Fig. 22).

Variation. Archer (1932), following Binney (1851: 97), speaks of the "narrow, thickened, rounded" peristome of *a. major* as a diagnostic feature. This holds true in some specimens, but many others have a relatively large aperture, almost like that in *a. albolabris.*

The *measured characters* are statistically correlated with each other and show irregular geographic variation. A few populations are morphologically intermediate between *a. major* and *a. albolabris*; these will be discussed in a later section.

Systematics. The conspecificity of *T. a. major* with *a. albolabris* is shown by the fact that they intergrade.

Triodopsis albolabris alleni (Wetherby, In Sampson)

Plate V: 4, 5

Mesodon albolabris Say var. *alleni* Wetherby, *In* Sampson, 1893, Ann. Rep. Geol. Surv. Arkansas for 1891, 2: 190. Eureka Springs, Carroll County, Arkansas. Paratype MCZ 79467.

Mesodon albolabris var. *minor* Wetherby, 1881, J. Cincinnati Soc. Nat. Hist. 4: 332. Eureka Springs, Carroll County, Arkansas. Not *Helix albolabris* var. *minor* Shuttleworth. Type not seen.

Definition. Triodopsis a. alleni is recognized here as defined by Pilsbry (1940). It contains those populations of the species which have mean values of 15–35 in character index. The method of computing character index is shown in Table XII. The subspecies slightly overlaps *T. a. albolabris* in character index, for reasons to be explained in a later section.

Description and differential diagnosis. Shell usually smaller and flatter than that of *a. albolabris*; width 23.3–30.1 mm; height 13.7–17.8 mm, height to width ratio 0.55–0.64; striated; intervals between striae shiny and smooth, or nearly so; grid, formed by intersecting spiral lines and transverse wrinkles, very faint; aperture oval, lip swelling thin, often with a very broad, low swelling near the columella; other characters as in *a. albolabris.*

Distribution. Triodopsis a. alleni is the western subspecies of *T. albolabris* (Fig. 22). It occurs west of the Mississippi River, from Minnesota to Iowa and south to Arkansas, or possibly to Texas (reported by Singley, 1893, quoted after Pilsbry, 1940: 841). Occasionally it is found on the eastern side of the river, as in Memphis, Shelby County, Tennessee.

The *measured material*, all MCZ, comes from the following localities: *Minnesota*: Hennepin County. *Illinois*: Hancock County. *Iowa*: Muscatine and Polk counties. *Missouri*: St. Louis, Johnson, and McDonald counties. *Kansas*: Miami County. *Arkansas*: Carroll and Washington counties. A total of 10 samples, 2–17 specimens each, 57 specimens altogether.

Ecology. Triodopsis a. alleni occurs predominantly in the oak-hickory forest region, but it penetrates the marginal zone of the prairies, and the maple-basswood and southeastern evergreen forests, also (Fig. 22). It ranges from 500 to slightly above 1500 feet elevation. It possibly shows ecological exclusion with *T. multilineata.*

Variation. The width and height of the shell are correlated. The width shows irregular geographic variation, the height to width ratio a gradual decrease from north to south. This is one of the few clines in *Triodopsis*.

Systematics. The conspecificity of *T. a. alleni* with *a. albolabris* is shown by their intergradation. (See below.)

Populations intermediate between *Triodopsis a. albolabris, a. major,* and *a. alleni*

Three populations from Lexington County, South Carolina, and Bradley and Warren counties, Tennessee (seven specimens altogether), are intermediate between *T. a. albolabris* and *a. major*. Their mean values in character index are 50–55; in *a. albolabris* they are 25–50, in *a. major*, 65–95.

Two populations from Knox and Washington counties, Tennessee, and one from Davidson County, Tennessee (28 specimens altogether), resemble the trans-Mississippian subspecies, *a. alleni*, in having semismooth (B) sculpture (below) and a flattened shell, respectively. In other characters, they are like *a. albolabris*. The mean value of these populations in character index is 25; in *a. alleni* it is 15–35, in *a. albolabris* 25–50.

Two populations from Jackson and Madison counties, Alabama (13 specimens), are large and have a thick lip swelling like *a. major*, but at the same time the shells are flat and have a semismooth sculpture (B), in which characters they approach *a. alleni*. Their mean values in character index are 45 and 50. The Jackson County population is currently recognized as *T. a. fuscolabris*[1] (Pl. V, figs 7, 8); it is not so recognized in this paper, however (see below).

All these localities lie in the zone of intergradation between *T. a. albolabris* and *a. major* (Fig. 22). This makes sense as far as the *albolabris-major* intergrades are concerned, but it leaves the *albolabris-alleni* and *major-alleni* intergrades unexplained. Perhaps there was a time when *a. alleni* was continuous in distribution with *a. albolabris* and *a. major* through the Tennessee-Alabama region, and the intergrading populations are remnants of this lost connection. The observation that *T. neglecta* shows the same pattern of variation lends support to this hypothesis. In that species, too, the Tennessee-Alabama populations resemble the isolated western subspecies in certain characters.

The intergradation is probably due to simple variation. Hybridization is unlikely, because the range of the variation of the intergrading populations is not wider than that of other, presumably "pure," parental ones (for further discussion, see p. 236). One can treat these populations as intergrades, or they may be considered parts of *a. albolabris* or *a. major*, in which they belong geographically. I prefer the first solution, although it does not really matter what these populations are called. The important thing is that intergradation exists among the three subspecies.

As mentioned earlier, one of the populations that intergrades between *a. major* and *a. alleni* is recognized in the present literature as a separate subspecies, *T. a. fuscolabris*. It does not deserve this status, however. Not only does it lack morphological distinction; it also has no range of its own (Fig. 22).

Variation of the character index in Triodopsis albolabris. Four characters were utilized in making up the character index: size (width), height and sculpture of the shell, and degree of development of the lower lip tooth or the swelling that replaces it. The first two characters were measured, the third and fourth graded by comparison to standard specimens. In sculpture, three grades were distinguished. Shells of grade A are smooth and shiny between the striae, or almost so. In grade B, a faint grid is visible between the striae, formed by the superimposition of fine spiral lines on wavy, transverse wrinkles. In grade C, the grid is coarse. Four grades of development of the lower lip tooth were distinguished: (1) no tooth, (2) small

[1] Pilsbry described this population as *Polygyra albolabris fuscolabris*, from Woodville, Jackson County, Alabama (1903, Proc. Acad. Nat. Sci. Philadelphia 55: 200). Type ANSP 66304.

tooth, (3) medium, and (4) large. Each character was scored according to the chart shown in Table XII, and the scores summed to obtain the character index.

According to the geographic variation of the character index, three subdivisions can be recognized in the species. One has mean values of 15–35, and occurs west of the Mississippi (Fig. 22). Another has mean values of 25–50, and occupies most of the range east of the Mississippi. The third has mean values of 65–95, and occurs in the southeastern tip of the range. Thus the geographic variation of the character index clearly supports the view that three subspecies are recognizable within the species.

The reason that *a. albolabris* and *a. alleni* overlap in character index is that size is included; *a. albolabris* and *a. alleni* completely overlap in this character. Size was included for the better separation of *a. major*; as all three subspecies intergrade, it was desirable to cover all three with the same character index.

Evolutionary relationships. T. a. albolabris occupies a central position geographically; the other two subspecies are peripheral. This would seem to indicate that the former subspecies gave rise to the others. Morphologically, however, each of the three subspecies intergrades with the others, which supports the notion that all three evolved from a common, widespread ancestor by adapting to local selective forces.

Summary. (1) *Triodopsis albolabris* consists of three intergrading subspecies: *a. albolabris*, *a. major*, and *a. alleni*. The currently recognized subspecies *T. a. fuscolabris* is not worthy of taxonomic recognition.

(2) *Triodopsis a. alleni* is geographically isolated from *a. albolabris* and *a. major*; the latter two subspecies are separated from one another by a zone of intergradation.

(3) *Triodopsis a. alleni* occurs only in areas of moderate elevation. The other two subspecies have a broader ecological spectrum. *Triodopsis a. alleni* may be ecologically exclusive of *T. multilineata*.

(4) The geographic variation is irregular in all characters in all three subspecies, except the height to width ratio in *a. alleni*, which varies clinally.

(5) The three subspecies probably evolved independently of one another from a common ancestral stock.

Triodopsis dentifera (A. Binney)
Plate VI: 1–3

Helix dentifera A. Binney, 1837, Boston J. Nat. Hist. 1: 494, pl. 21. "In the state of Vermont, on the eastern slope of the Green Mountains." The possible type is a specimen in the MCZ collection, collected by A. Binney in "Vermont," labelled as "cotype (?)"; MCZ 152236, A. F. Gray Collection.

Mesodon dentiferus var. *major* Ancey, 1887, Conch. Exch. 1: 55. "Mountains of east Tennessee." Type not seen.

Definition. The taxon is used here as recognized in the current literature.

Description. Shell width 19.5–27.6 mm; height 10.6–15.6 mm, height to width ratio 0.52–0.57; no umbilicus; embryonic whorls 1.4–1.5, striated below suture; striation on subsequent whorls becoming more pronounced, 3–4 striae per millimeter on last whorl; intervals of striae with fine grid formed by intersecting spiral and transverse lines (about 40 spiral lines per millimeter); after breakage, deep spiral grooves appear; aperture oval, lip swelling strong and flat; no lip teeth; parietal lamella small.

Differential diagnosis. Triodopsis dentifera is very similar to *T. a. albolabris*, but its shell is smaller and flatter, and its lip swelling is heavier. In addition, it has a parietal lamella, whereas *a. albolabris* very rarely does.

Distribution. Triodopsis dentifera ranges from Quebec to Pennsylvania (Fig. 23). It also occurs farther south in the Tennessee-North Carolina region. Taft (1961) reports it from Hamilton County, Ohio. The latter areas seem to be isolated from the main part of the range. This pattern may imply that the species is in the withdrawal stage, but this is not certain. In Ohio, the species is adjacent to the related species, *T. multilineata.* It appears that the two forms are replacing one another geographically.

The *measured material*, all MCZ, comes from the following localities: *Quebec*: Labelle County. *New Hampshire*: Cheshire and Grafton counties. *Vermont*: Lamoille and Windsor counties; one specimen (? cotype) from Vermont, without detailed locality. *New York*: Franklin County. *Pennsylvania*: Wayne and Allegheny counties. *North Carolina*: Watauga County. A total of 13 samples, 1–5 specimens each, 24 specimens altogether.

Ecology. Triodopsis dentifera is mainly found in the cool northeastern regions of the continent, covered by northern hardwood forests (Fig. 23). Only sporadic records are known from more southern regions, from oak-chestnut and mixed mesophytic forests. All localities lie above 500 feet elevation.

Variation. The variation of the species conforms to the pattern usually found in *Triodopsis*: width and height of shell are correlated, and the geographic variation of both characters is irregular. The variation is limited, as expected from the small size of the population.

Systematics. Triodopsis dentifera var. *major* was described from the mountains of eastern Tennessee. The type specimens are not known, but supposedly they were large (28 mm), dark colored shells, with deep spiral lines on the lower surface. Currently, *major* is considered synonymous with *dentifera*, for the reason that specimens of *dentifera* from Banner's Elk, Watauga County, North Carolina, are nearly as large (26.1–26.5 mm) as *major* was supposed to be, but otherwise are "normal" *dentifera.* I may add that the deep spiral lines, thought to be of diagnostic value, probably resulted from an injury, as these lines have been found in many injured specimens of the *albolabris*, *fosteri*, and *mullani* groups (Pl. V, fig. 11).

Summary. Triodopsis dentifera is a monotypic species. Its population is small, its variation narrow and irregular. Geographically, it replaces the related species *T. multilineata.*

Triodopsis multilineata (Say)
Plate VI: 4–7

Helix multilineata Say, 1821, J. Acad. Nat. Sci. Philadelphia 2: 150. Type unknown. Say gave "Illinois and Missouri" as the type locality; I restrict it to Hamilton, Hancock County, Illinois.

Polygyra multilineata subsp. *algonquinensis* Mason, 1906, Nautilus 19: 141. Marshy and boggy places around roots of willows; Algonquin, McHenry County, Illinois. Types MCZ 148145 and ANSP 91193.

Polygyra multilineata var. *chadwicki* Ferriss, 1907, Nautilus 21: 37. Banks of Kaw River, near Lawrence, Douglas County, Kansas. Paratypes MCZ 222099.

Polygyra multilineata var. *altonensis* F. C. Baker, 1920, Nautilus 34: 65. From loess, Alton, Madison County, Illinois. Type not seen.

Polygyra multilineata var. *wanlessi* F. C. Baker, 1928, Nautilus 41: 132. Peorian loess, east of Havana, Fulton County, Illinois. Type not seen.

Definition. Triodopsis multilineata as used here includes the currently recognized taxa *multilineata*, *m.* forma *algonquinensis*, and *m.* forma *chadwicki.*

Description. Shell width 16.2–28.1 mm; height 10.0–18.2 mm, height to width ratio 0.55–0.71; no umbilicus; embryonic whorls 1.4–1.5, smooth or finely striated below suture (20–25 striae per millimeter); striation becoming more pronounced on subsequent whorls, about two striae per millimeter on last whorl; third whorl with a grid formed by extremely delicate spiral and transverse lines; grid on subsequent whorls somewhat coarser, but still very fine (30 spiral lines per millimeter); shell banded with dark reddish brown bands, rarely uniformly dark reddish brown or horn colored; after breakage, deep spiral grooves may develop; aperture oval, without lip teeth; parietal lamella, or a callosity in its place, may be present.

Differential diagnosis. The thin lip and the banded shell readily distinguish this species from *T. albolabris* or *T. dentifera.*

Distribution. Triodopsis multilineata lives in the northern midwestern states,

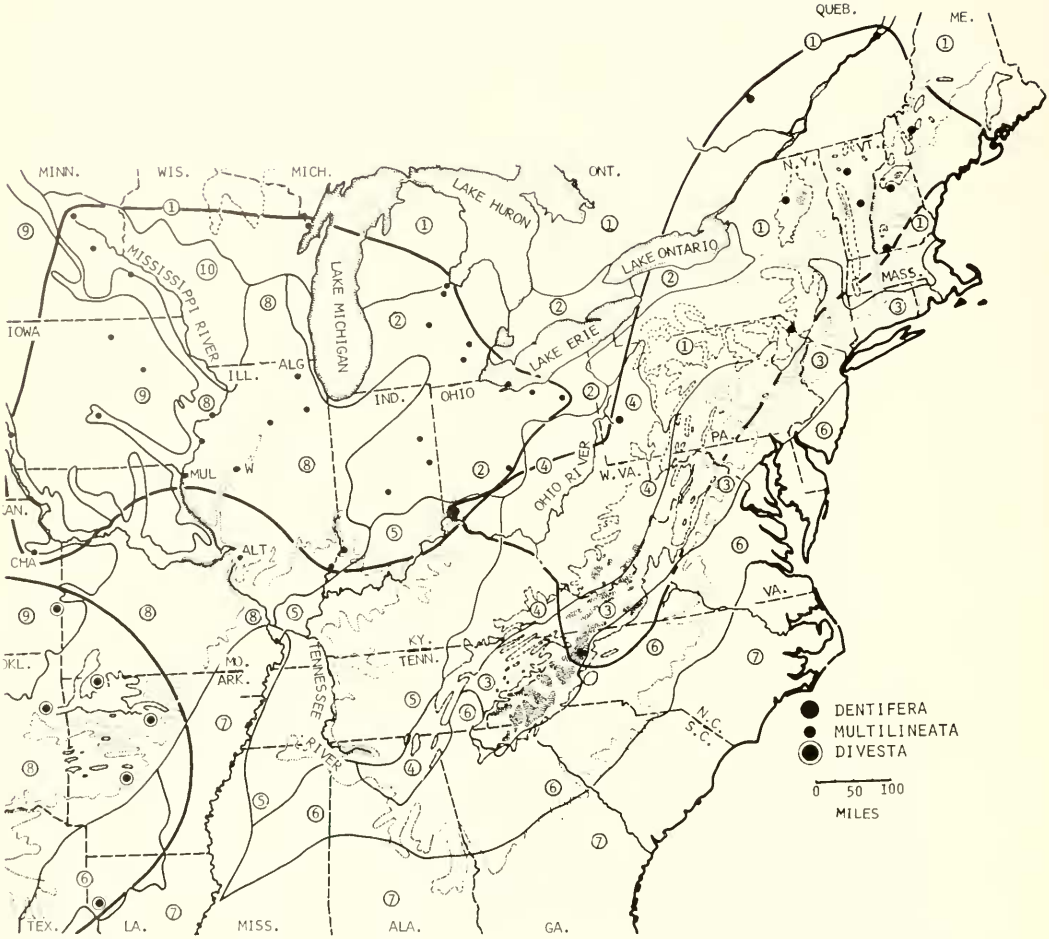

Figure 23. Distribution of *Triodopsis dentifera*, *multilineata*, and *divesta*. Thick, solid line surrounds the range of the three species. ALG., type locality of *algonquinensis*; ALT., *altonensis*; CHA., *chadwicki*; W., *wanlessi*; these forms are considered synonymous with *multilineata*; MUL., *multilineata*. Other symbols refer to elevation, forest types, and state boundaries, as explained in Figure 3.

from Minnesota east to Michigan and Ohio and south to Kansas. Its range is adjacent to that of *T. dentifera* in the east and *T. divesta* in the west. The three forms apparently replace each other geographically (Fig. 23).

The *measured material* comes from the following localities: *Michigan*: Menominee, Huron, Saginaw, Oakland, Washtenaw, Clinton, Kent, and Calhoun counties. *Minnesota*: Stearns, Hennepin, and Goodhue counties. *Ohio*: Portage, Lorain, Ottawa, Franklin, and Hamilton counties. *Indiana*: Wells, Randolph, Marion, and Knox counties. *Illinois*: McHenry, Will, LaSalle, Mercer, Hancock, and Wabash counties. *Iowa*: Cerro Gordo, Black Hawk, Scott, Polk, and Pottawattamie counties. *Kansas*: Douglas County. A total of 32 samples, 2–25 specimens each, 230 specimens altogether.

Ecology. *Triodopsis multilineata* lives in oak-hickory, beech-maple, and maple-basswood forests (Fig. 23). A few localities also occur in northern hardwoods, in the western mesophytic forests, and in the prairies. The prairie localities, however, may be the result of the inaccuracy of the map; its scale is too large to show very small patches of woods. All localities lie higher than 500 feet.

Various collectors have observed that the species prefers river banks and other moist places. It shares this preference with *T. a. alleni*, a sympatric form. Although I do not have personal experience with them, and the museum labels do not say it explicitly, I assume that the two species live in habitat exclusion—that is, in any given habitat either one of them may occur, but not the two together. This assumption is based on the behavior of numerous other sympatric species pairs of *Triodopsis*, such as *tridentata-juxtidens, juxtidens-fallax*, etc.

It may be that *T. multilineata* is also ecologically exclusive of *T. dentifera* and *T. divesta*. This could be inferred, at least, from the fact that it replaces these forms geographically (Fig. 23). Exclusion seems, however, less certain in these than in some other cases, since the three forms are separated from one another by gaps. Thus they are not in competition with one another, and without competition, one cannot assume exclusion.

Triodopsis multilineata has the interesting habit of gathering into groups for hibernation. Pilsbry (1940: 848) quotes Dr. Kirtland when writing: "At the approach of winter it [*T. multilineata*] retreats to the carex-tops, where several dozen may be found together in a torpid state, with the mouth of their shells closed with an epiphragm. . . . The numbers collected in these retreats are sometimes agglutinated into one mass." I observed hibernation in groups also in several species of the family Zonitidae.

Variation. Aperture: A small or medium large parietal lamella appears in specimens collected at Lawrence, Douglas County, Kansas. These specimens have been described as *T. m.* forma *chadwicki*. This is not justified in my opinion, however. For explanation, see systematics, below.

Color: The shell is usually ornamented with six to eight reddish brown bands on a light horn ground color. The bands may decrease in number until they entirely disappear, or may expand until the shell becomes entirely reddish brown. Banded and unicolored shells occur together in many populations. Despite this, however, the light shells were at one time recognized as var. *alba* or *albina*, the red ones as var. *rubra* or *rufa* or *unicolor*. Currently, these names are considered synonyms.

Among the *measured characters*, the width of the shell correlates with the height. Geographically, both width and the height to width ratio vary irregularly.

Systematics. Triodopsis m. forma *chadwicki* from Lawrence, Douglas County, Kansas, has been separated from the nominate form of *multilineata* because it has a parietal lamella and is uniformly dark reddish brown. These features occur, however, in several, widely separated populations of *multilineata*; also, not all specimens of *chadwicki* exhibit these features. In consequence, *chadwicki* is considered synonymous with *multilineata*.

Triodopsis m. forma *algonquinensis* (Pl. VI, fig. 4) from Algonquin, McHenry County, Illinois, is said to be an ecological form of the prairie region, which is characterized by its small body size, high spire, and dark color (Pilsbry, 1940: 850). My measurements on size and height do not show any significant difference between prairie and non-prairie populations, and the color variation, as shown above, is inconsequential. For these reasons, I propose to make *algonquinensis* synonymous with *multilineata*.

Following Shimek (1936) and Pilsbry (1940: 850), we may consider var. *wanlessi*, a loess form, identical with *algonquinensis*. "The fossil condition of *wanlessi* is about all that constantly separates them" (Pilsbry, *ibid.*). Since, as demonstrated above, *algonquinensis* is synonymous with *multilineata*, *wanlessi* is also a synonym.

Triodopsis m. var. *altonensis*, another loess form, is claimed to be "larger . . . more gibbous . . . [and the] spire more depressed. . . ." than the typical form. Specimens as large and gibbous as *altonensis* occur, however, in several loess and Recent populations. Therefore, in agreement with Pilsbry (1940: 849), we may consider the name *altonensis* synonymous with *multilineata*.

Summary. (1) *Triodopsis multilineata* is a monotypic species; the forms *chadwicki* and *algonquinensis*, and varieties *wanlessi* and *altonensis* are individual or ecological variants of *multilineata*, and therefore synonymous with it.

(2) Geographically, *Triodopsis multilineata* replaces the related species *T. dentifera* and *T. divesta*. It prefers moist habitats. It hibernates in aggregates, a habit unique in *Triodopsis*.

(3) Another unique feature is its banded shell, the bands of which exhibit great variation in number and extent. All characters show irregular geographic variation.

Triodopsis divesta (Gould)
Plate VI: 8–10

Helix divesta Gould, 1851, *In*: A. Binney, The Terrestrial Air-breathing Mollusks of the United States 2: 358, and 3: 27, pl. XIIIa, fig. 2. Substitute name for *Helix abjecta* Gould. "Arkansas." Cotype MCZ 72831.

Helix abjecta Gould, 1848, Proc. Boston Soc. Nat. Hist. 3: 40. "South-western States." Not *Helix abjecta* Lowe, 1831.

Definition. The taxon *Triodopsis divesta* is recognized here as conventional.

Description. Shell width 16.9–19.5 mm; height 8.7–11.8 mm, height to width ratio 0.49–0.67; no umbilicus; embryonic whorls 1.3–1.5, finely striated (25 striae per millimeter); subsequent whorls with stronger, more widely spaced striae (3–4 per millimeter); intervals between striae with short and wavy transverse wrinkles, arranged loosely in spiral bands, which may be separated from one another by smooth bands; spiral lines also present, but so extremely fine that they are barely visible, even on fresh specimens; last whorl slightly angular at its periphery; aperture oval, with a lip swelling, but without lip teeth or parietal lamella.

Differential diagnosis. The shell of *Triodopsis divesta* is similar to that of *T. multilineata*, but is not banded; it has a distinctive microscopic sculpture.

Distribution. *Triodopsis divesta* occurs west of the Mississippi, from Kansas to Louisiana. It does not enter the Ozark Mountains proper, but stops at their foot (Fig. 23). Its range is adjacent to that of the related species *T. multilineata*, and the two species replace one another geographically.

The *measured material*, all MCZ, comes from the following localities. *Arkansas*: Van Buren, Carroll, and Garland counties; cotype from "Arkansas," without more detailed locality. *Kansas*: Bourbon County. *Oklahoma*: Cherokee County. *Louisiana*: De Soto County. A total of 7 samples, 1–13 specimens each, 24 specimens altogether.

Ecology. *Triodopsis divesta* lives in oak-hickory and southeastern evergreen forests; it also seems to penetrate the eastern margin of the prairie land; however, the localities from the prairie may be patches of woods too small to be shown on the map (Fig. 23). The species seems to prefer moderate elevations between 500 and 1500 feet. In this respect, it is similar to the allied species *T. multilineata* and *dentifera*.

It is possible that *T. divesta* shows habitat exclusion with *T. a. alleni*, which it completely overlaps. I do not have enough data to prove this, however.

Variation. The shell width is correlated with height; the width and the height to width ratio show irregular geographic variation.

Summary. *Triodopsis divesta* is a monotypic species. It shows geographic replacement with *T. multilineata*, and possibly habitat exclusion with *T. a. alleni*. Its geographic variation is irregular.

Evolutionary relationships among the members of the albolabris complex. *Triodopsis albolabris* displays a great overall similarity to *dentifera*. On this basis, the two can be considered very closely related. It is not known, however, whether *dentifera* evolved from *albolabris*, or both developed from a common ancestor, because according to its distributional pattern, *dentifera* may equally well be a relic or a young species. Uncertainties beset the origin of *multilineata* and *divesta*, also. These species do not show clear affinities to one another, nor to *albolabris* or *dentifera*. We can only say that they probably evolved long ago from a *Neohelix* stock.

Subgenus *CRYPTOMASTIX*

Cryptomastix Pilsbry, 1939, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (1): XVII.

Type. Triodopsis mullani olneyae (Pilsbry) (a synonym of *T. m. mullani*, below), by original designation.

Cryptomastix differs anatomically from other subgenera of *Triodopsis* by having a flagellum and a twin pilaster in the genital apparatus. For this reason, and because it is widely isolated geographically from the other subgenera, it might be better considered a separate genus. I follow the current classification, however, and include it in *Triodopsis* because of considerations explained elsewhere (p. 148).

The subgenus consists of one species complex, the *mullani* complex, and a single isolated species, *germana*.

THE *MULLANI* COMPLEX

The *mullani* complex consists of three species: *mullani*, *sanburni*, and *devia*. *Triodopsis mullani* has two subspecies, *m. mullani* and *m. harfordiana*, that hybridize with each other. *Triodopsis sanburni* and *devia* are monotypic.

Triodopsis mullani (Bland and Cooper)
Triodopsis mullani mullani (Bland and Cooper)

Plate VII: 8–10, 12–14

Helix mullani Bland and Cooper, 1861, Ann. Lyc. Nat. Hist. New York 7: 363, pl. 4, figs. 16, 17. Near Coeur d'Alene Mission, Coeur d'Alene Mountains, Idaho. Topotype, labelled "probably one of original lot," ANSP 1901.

Triodopsis hemphilli W. G. Binney 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 38, pl. 1, fig. 17. Kingston, Shoshone County, Idaho. Type ANSP 11106.

Helix binominata Tryon, 1887, Man. Conch. 3: 146, pl. 38, figs. 98, 99. Substitute name for *Triodopsis hemphilli* W. G. Binney.

Polygyra (*Triodopsis*) *mullani* var. *olneyae* Pilsbry, 1891, Nautilus 5: 47. Spokane, Spokane County, Washington. Type ANSP 11112.

Triodopsis mullani Bland, var. *blandi* Hemphill, 1892, *In*: Binney, 4th Suppl., Bull. Mus. Comp. Zool. 22: 184. Post Falls, Kootenai County, Idaho. Type not seen.

Triodopsis populi Vanatta, 1924, Proc. Acad. Nat. Sci. Philadelphia 76: 26, figs. 3,4. Cottonwood Tree Canyon, on Snake River, 50 miles south of Lewiston, Nez Perce County, Idaho. Type ANSP 132939.

Polygyra mullani subsp. *hendersoni* Pilsbry, 1928, Proc. Acad. Nat. Sci. Philadelphia 80: 178, fig. 206. The Dalles, Wasco County, Oregon. Type ANSP 145479.

Helix (*Mesodon*) *mullani* Bland and Cooper, var. *oregonensis* Ancey, 1882, Le Naturaliste 2: 29. "Oregon oriental." Not *Helix oregonensis* Lea, 1839.

Triodopsis mullani subsp. *tuckeri* Pilsbry and Henderson, 1930, Nautilus 44: 121, pl. 5, figs. 8–10. On the Clearwater River near the junction of Fourth-of-July Creek, Idaho. Cotype ANSP 152334.

Triodopsis mullani subsp. *latilabris* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 863, fig. 500. Lower two or three miles of John Day Creek, Idaho. Type ANSP 175777.

Definition. Triodopsis m. mullani combines the forms classified by Pilsbry (1940) as *T. m. mullani*, *m. tuckeri*, *m. latilabris*, *m. olneyae*, *m. hemphilli*, *m. hendersoni*, *m. blandi*, and *T. populi*. It contains all those populations of the species which have mean values of 40–100 in character index. The method of computing character index is shown in Table XIII.

Description. Shell width 12.6–19.0 mm; height 6.2–10.6 mm, height to width ratio 0.48–0.60; umbilicus narrow to moderately wide, slightly or sometimes almost completely covered by reflected edge of lower lip; whorl number 5.1–5.9, whorl to width ratio 0.31–0.42; embryonic whorls 1.4–1.5,

Table XIII

Chart for Computing Character Index in *Triodopsis mullani*. Method of Calculation: a Specimen with a Shell Width of 18.6 mm, a Height of 10.2 mm, and a Whorl to Width Ratio of 0.32 was Scored 40 + 30 + 30 = 100, the Available Maximum Score.

Score	Width	Height	Whorl to width ratio	
0	8.6–9.7	4.0–4.9	0.50–0.53	*m. harfordiana*
5	9.8–10.9	5.0–5.9	0.47–0.49	↑
10	11.0–12.1	6.0–6.8	0.44–0.46	
15	12.2–13.2	6.9–7.7	0.41–0.43	
20	13.3–14.3	7.8–8.6	0.38–0.40	
25	14.4–15.4	8.7–9.6	0.35–0.37	
30	15.5–16.6	9.7–10.6	0.31–0.34	
35	16.7–17.8			↓
40	17.9–19.0			*m. mullani*

striated below suture; striae usually breaking into granules towards their ends; rest of embryonic whorls smooth; subsequent whorls covered by alternating weaker and stronger striae; intervals of striae with fine spiral lines, about 30 per millimeter; between these lines even finer transverse lines and on some specimens papillae also present; papillae reportedly with hairs, but I have not seen any; aperture triangular or trapezoid or oval; lip swelling thin to very thick, upper lip swelling sometimes bulging in region of upper lip tooth; lip teeth moderately large, small, or absent; lower lip tooth located close to right corner of aperture; parietal lamella very small to moderately large.

Distribution. Triodopsis m. mullani is confined to three more or less isolated areas between the Cascade Range and the Rocky Mountains (Fig. 24). One is at the eastern foothills of the Cascade Range, where the Columbia River crosses the range. Another lies in the region of the Spokane River, and the third in the region of the Snake River. Both of these lie on the western slopes of the Rockies. The low area between the Cascade Range and the Rockies remains unoccupied.

Triodopsis m. mullani is entirely allopatric with *T. devia*, and sympatric with *T. sanburni*, which are closely related species.

The *measured material*, all MCZ, comes from the following localities: *Montana*: Lincoln County. *Idaho*: Boundary, Shoshone, Kootenai, Latah, Washington, and Gem counties. *Washington*: Spokane County. *Oregon*: Umatilla and Wasco (2 samples) counties. A total of 11 samples, 1–11 specimens each, 37 specimens altogether.

Ecology. Triodopsis m. mullani occurs predominantly between 1500 and 6000 feet elevation. Extreme localities may occur, however, as low as 500 feet (Fig. 24). Pilsbry (1940: 861) reports that H. B. Baker found "typical *mullani*" at 5400–5600 feet, in larch-pine-hemlock forest, on schistose rocks, at rock slides, and springs around Twin Lakes, Stephens Peak, Shoshone County, Idaho.

The exact altitude of many localities is not known. The available data seem to indicate, however, that the variation of the aperture is correlated with elevation. See below.

Variation. In view of the fact that *Triodopsis m. mullani* is a relatively small population, its variation is unexpectedly great. This applies particularly to the aperture and the umbilicus.

Aperture: The lip swelling may be thick or thin, lip teeth moderate or small or entirely lacking, parietal lamella moderate or small. In all cases the extreme specimens intergrade. Considerable variation may occur within a single local population. Those populations with the thickest lip swelling and largest lip teeth seem to concentrate in the higher regions of the range, while those with a thinner lip swelling and small or obsolete teeth live in the lower regions. If this generalization is valid, *T. m. mullani* can be said to show the same trend as was observed in *T. tridentata*, *fallax*, and the *n. vulgata-fraudulenta* group, in which montane populations also have a stronger armature than do lowland populations.

The *sculpture* consists of striae, fine lines, and papillae. The striation is well

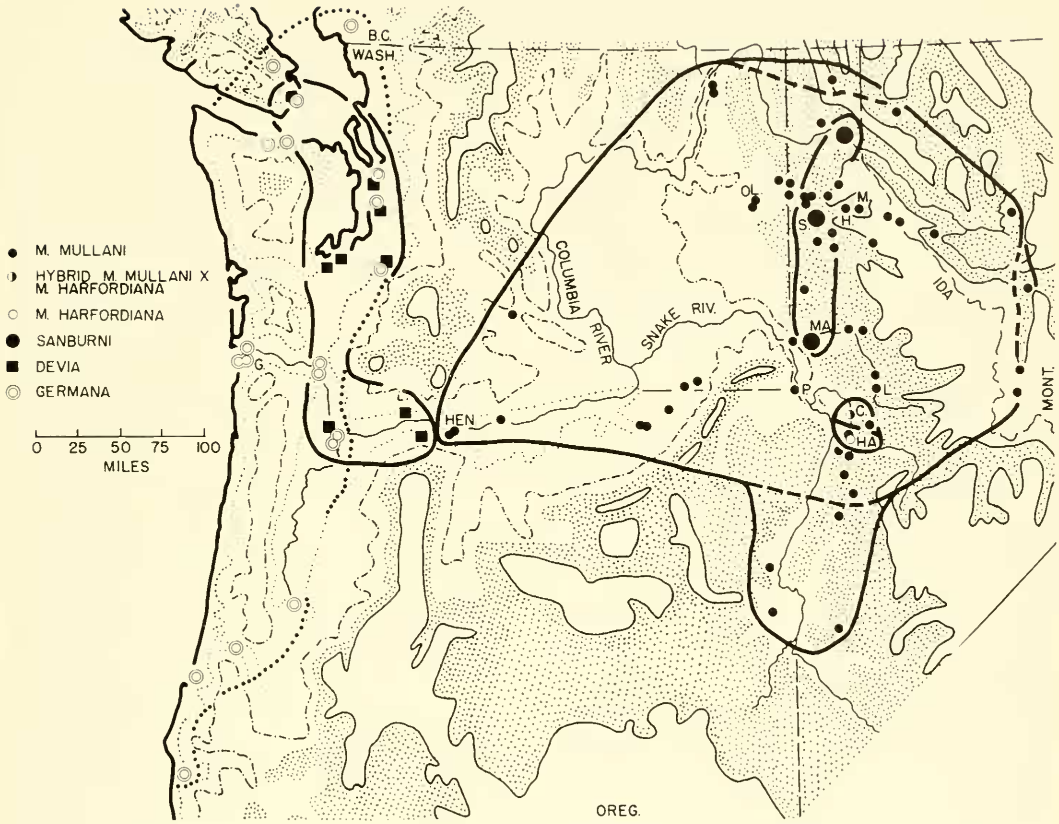

Figure 24. Distribution of *Triodopsis mullani, devia, sanburni,* and *germana.* Thick, solid lines surround the range of *m. mullani,* hybrid *m. mullani* × *m. harfordiana, m. harfordiana, sanburni,* and *devia;* thick, dashed line surrounds the range of *olneyae,* formerly recognized as a subspecies of *mullani,* here considered synonymous with *m. mullani;* dotted line surrounds the range of *germana.* G., type locality of *germana;* MA., *magnidentata,* considered synonymous with *sanburni;* S., *sanburni;* C., *clappi,* considered hybrid *m. mullani* × *m. harfordiana;* HA., *m. harfordiana;* H., *hemphilli;* HEN., *hendersoni;* L., *latilabris;* M., *m. mullani;* OL., *olneyae;* P., *populi;* the last six forms are all included in *m. mullani.* Elevation: . . . . . 656-foot contour line; . —— . —— . 1640–foot; area over 3281 feet is dotted; area over 6562 feet, blank, surrounded by thin, solid line. State boundaries are marked by thin, dashed lines.

developed on the upper side, where stronger and weaker striae alternate rather regularly (each strong stria is followed by two weak ones). On the lower side of the shell, the striation is nearly effaced. The intervals of the striae are covered by fine spiral lines, and the intervals of the latter are covered by even finer transverse lines. The spiral lines are pinched together at the papillae. The papillae are supposed to bear hairs, but I have not seen any with hairs. It is possible that in the shells examined they were worn off. Deep spiral lines also may be occasionally present. They may extend over the entire last whorl (or whorls), or may be restricted to a smaller or larger portion thereof, behind the aperture. These lines always follow a severe breakage in the shell and, therefore, are apparently the result of an injury to the mantle edge. This situation is similar to that found in *T. fosteri* and in the *T. albolabris* group.

The *umbilicus* may be very narrow to wide open. Considerable variation may occur within a single population. It is important to point out that there is no real correlation between the variation of the umbilicus and the aperture. For instance, specimens with either a narrow or a wide umbilicus may have a weak aperture.

The *measured characters*, such as width, height, and whorl number, are statistically correlated with one another, and show irregular geographic variation.

The *character index* shows irregular geographic variation.

Systematics. Triodopsis m. mullani combines eight taxa ranked as separate subspecies or species in Pilsbry's classification (1940). These are: *Triodopsis m. mullani, m. olneyae, m. latilabris, m. tuckeri, m. blandi, m. hendersoni, m. hemphilli*, and *T. populi*. This large-scale lumping is necessitated by both morphological and distributional evidence. Because of the nature of the argument, I will not take up each taxon separately, but will discuss them together.

(1) Morphological evidence. In respect to the aperture and the umbilicus, the eight taxa form an uninterrupted morphological series. The aperture series starts with *hendersoni, blandi*, and *populi*, which totally lack lip teeth and have a thin lip swelling. It continues with *tuckeri* and *hemphilli*, with small lip teeth and a thin lip swelling; *olneyae*, having small to moderate lip teeth and a medium thick lip swelling. It ends with *latilabris* and *mullani*, which have small to moderate lip teeth and a very thick lip swelling. The umbilicus series starts with those specimens of *hemphilli* with a nearly imperforate shell. It continues with other specimens of *hemphilli*, and with those of *mullani, tuckeri*, and *hendersoni*, all of which have a narrow umbilicus. These are followed by *latilabris*, which has a narrow to medium wide umbilicus, and finally by *blandi, populi*, and *olneyae*, which have a medium wide umbilicus. In summary:

Aperture series: *hendersoni—blandi—populi—tuckeri—hemphilli—olneyae—latilabris—mullani.*

Umbilicus series: *hemphilli—mullani—tuckeri—hendersoni—latilabris—blandi—populi—olneyae.*

There are no convenient breaking points whereby the series could be subdivided. Nor does the aperture series coincide with the umbilicus series. Subdivisions based on the aperture are, therefore, in conflict with those based on the umbilicus. Such continuous and discordant variation should not be used for the separation of subspecies.

(2) Distributional evidence. (a) Populations with small or large lip teeth, or with a narrow or a wide umbilicus, do not form geographical races; instead, the aperture varies more or less in correlation with elevation, and the umbilicus varies irregularly. (b) One of the eight taxa in question, *olneyae*, completely overlaps *latilabris, mullani, tuckeri*, and *populi*, and partially overlaps *blandi, hemphilli*, and *hendersoni* (Fig. 24). Overlapping populations which have no morphological distinction should not be considered separate subspecies without further evidence. There is no such evidence in the present case.

Pilsbry himself was aware of this situation. On page 860 of his book (1940) he writes: "In fact, *mullani* and *hemphilli* seem to be merely the end forms in a continuous series, found in the same colonies, not really different races." On page 862: "In any large lot the variation from *mullani* to *hemphilli* is really continuous." On page 865: "In Idaho the line between *olneyae* and *hemphilli* is practically wiped out, since specimens referable to both or either, often occur in the same lots." On page 865: South of Stites, Idaho County, Idaho, ". . . the shells are small, rather delicate, thin, and strongly depressed as in *clappi*, but the callus in the basal lip is about as in the larger *olneyae*. . . ." On page 867: "In this area [Snake River Valley, around Weiser, Washington County, Idaho] it becomes a nice question where to draw the line between *hendersoni* and *clappi*." It is not at all clear to me why, in the face of such statements, he maintained the subspecific status of these forms, even adding new forms as late as 1940.

According to Pilsbry's classification, two more subspecies belong to *T. mullani*: *m. magnidentata* and *m. clappi*. In my opinion, *magnidentata* is identical with *T. sanburni*, and I therefore consider it a synonym of that species (p. 229). *Triodopsis m. clappi* is apparently a hybrid between *m. mullani* and *m. harfordiana*, and I therefore consider this name invalid.

Triodopsis mullani harfordiana W. G. Binney

Plate VII: 4–6

Triodopsis harfordiana W. G. Binney, 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 37. Salmon River, Idaho. Type MCZ 12674.

Helix salmonensis Tryon, September 2, 1887, Man. Conch., (2) 3: 146, pl. 38, figs. 96, 97. Salmon River, Idaho. Substitute name for *Triodopsis harfordiana* W. G. Binney 1886. Type ANSP 11116.

Helix commutanda Ancey, December 1887, Conch. Exch. 2: 79. Substitute name for *Triodopsis harfordiana* W. G. Binney 1886.

Definition. *Triodopsis m. harfordiana* corresponds to *T. harfordiana* of Pilsbry (1940: 869). It contains those populations of the species which have mean values of 0–5 in character index. The method of computing character index is shown in Table XIII (p. 224).

Description. Shell width 8.6–10.1 mm; height 4.0–4.8 mm, height to width ratio 0.43–0.51; umbilicus wide, cylindrical; number of whorls 4.6–5.1, whorl to width ratio 0.47–0.53; embryonic whorls 1.4–1.5, striated below suture, smooth elsewhere; striae closely spaced on subsequent whorls, about 9–10 per millimeter; all striae about equally strong, and equally well developed on upper and lower surfaces of shell; in spaces between striae fine spiral and transverse lines and hair-bearing papillae may be present (contrary to Pilsbry's claim, 1940: 870); last whorl sometimes slightly angular at its periphery; aperture low trapezoid; lip swelling moderately thick; upper lip tooth moderately large, lower long, bladelike; parietal lamella straight and long, pointing above or at upper lip tooth.

Differential diagnosis. *Triodopsis m. harfordiana* differs from *m. mullani* in its smaller, flatter, and more evenly striated shell, more closely arranged hairs, and wider and more cylindrical umbilicus.

Distribution and ecology. *Triodopsis m. harfordiana* is confined to the valley of the Salmon River, a tributary of the Snake River (Fig. 24). The Salmon River cuts deep into the mountains; the *m. harfordiana* population therefore seems to be well isolated from the rest of the species. The isolation cannot be a permanent one, however, since invasions have occurred repeatedly (see discussion of hybrids).

The *measured material* (5 samples, 1–3 specimens each, 9 specimens altogether, all MCZ) comes from the Salmon River Valley, probably north of Lucile, Idaho County, Idaho; exact localities are not given. Some samples were collected on the river banks. The elevation of the area is about 2000–2500 feet.

Variation. Because the total population is small and the area restricted, the variation of *Triodopsis m. harfordiana* is very narrow. A positive correlation is evident, however, between width, height, and whorl number.

Systematics. *Triodopsis m. harfordiana* is considered conspecific with *m. mullani* because they hybridize. The occurrence of hybridization is indicated by morphological studies, and is supported by the pattern of distribution.

The nomenclature of *T. m. harfordiana* has had a rather confusing history, which was well summarized by Pilsbry (1940: 870). When W. G. Binney first mentioned the name *Triodopsis harfordiana*, in 1878, he gave J. G. Cooper as the author and, like Cooper, included in the species the Californian polygyrid *Daedalochila harfordiana*. Having noticed his error, in 1886 Binney gave a new description and a figure for *Triodopsis harfordiana*, excluding *Daedalochila harfordiana*, and omitting Cooper as author. In 1887, both Tryon and Ancey renamed *T. harfordiana*, because they argued that the name was a homonym of *Helix harfordiana*. Tryon's name, *salmonensis*, was used subsequently in the literature until 1923, when the Nomenclature Committee of the American Malacological Union decided to drop it in favor of Binney's *harfordiana*. The Committee felt that Binney in 1886 had described a "new" species; therefore his name was valid. This usage has been accepted ever since.

Hybrid populations between *Triodopsis m. mullani* and *m. harfordiana*

Plate VII: 7, 11

In a sample from Salmon River, Idaho County, Idaho, "good" *m. mullani* and intermediates between *m. mullani* and *m. harfordiana* occur together. The mean value of this sample in character index is 35, that of *m. mullani* is 40–100, of *m. harfordiana*, 0–5. Another sample, collected in the same area, contains one intermediate specimen and two "good" *m. harfordiana*; the mean value of this sample is 15. A third sample, also from the Salmon River, consists exclusively of intermediate specimens; the mean value is 35. A total of 3 samples, 3–6 specimens each, 12 specimens altogether.

The first two samples are more variable than any other sample of the species, which indicates that they are of hybrid origin. Their geographical distribution is consistent with this statement: they occur in areas where both *m. mullani* and *m. harfordiana* live in proximity (Fig. 24). It appears probable that after an earlier period of isolation, during which *m. mullani* and *m. harfordiana* differentiated into separate subspecies, *m. mullani* secondarily "invaded" the area of *m. harfordiana*. Because of a lack of internal isolating mechanisms, this resulted in hybridization between the two populations.

The third sample shows only normal variation. But it also is considered hybrid, because it is very similar to the putative hybrids, and occurs in the same area.

The intergradation between *mullani* and *harfordiana* (old usage) indicates that these taxa are, in reality, conspecific. Workers who treated them as separate species overlooked the intergradation. The correct names for *mullani* and *harfordiana* are, accordingly, *m. mullani* and *m. harfordiana*. The sample that contains exclusively intermediate specimens was described as *T. m. clappi* (Hemphill, 1897, Nautilus 11: 74; type ANSP 71479). This name is to be considered invalid.

Evolutionary relationships. Triodopsis m. harfordiana can be considered a geographic isolate of *m. mullani*. As may be recalled, *m. mullani* occupies the whole valley of the Snake River, whereas *m. harfordiana* is confined to the valley of the Salmon River, a small tributary thereof. On this basis, it appears likely that *m. harfordiana* developed from *m. mullani*.

Triodopsis m. mullani lives in a mountainous area. The higher mountain ridges are likely to impede gene flow between the various parts of the population or even between neighboring demes. Thus, the Spokane River population is pretty well isolated from the population living in the upper valley of the Snake River (Fig. 24). Not ridges, but the wide open basin of the Columbia River separates the Cascade Range and the Rocky Mountain populations. These groups may in time become separate subspecies or even species.

Summary. (1) *Triodopsis mullani* has two subspecies: *m. mullani* and *m. harfordiana*. *Triodopsis m. mullani* combines the former *m. mullani*, *m. latilabris*, *m. tuckeri*, *m. olneyae*, *m. hemphilli*, *m. hendersoni*, *m. blandi* and *T. populi*. *Triodopsis m. harfordiana* corresponds to the former *T. harfordiana*. The former *T. m. magnidentata* is excluded from the species, and is attached to *T. sanburni* as a synonym. The former *T. m. clappi* is considered an invalid name, since it was given to a hybrid population.

(2) The two recognized subspecies are quite distinct morphologically. Their con-

specificity is shown by the fact that they hybridize.

(3) *Triodopsis m. mullani* occurs in three isolated areas in the basin of the Columbia River. *Triodopsis m. harfordiana* is confined to a small tributary of this river. The hybrids occur near *m. harfordiana.*

(4) *Triodopsis m. mullani* occurs predominantly between 1500 and 6000 feet; rarely, however, it may occur as low as 500 feet. *Triodopsis m. harfordiana* and the hybrids occur around 2000–2500 feet.

(5) The variation of *T. m. mullani* is greater than would be expected from its relatively small population and the relatively limited area it occupies. The variation of the aperture may be correlated with the elevation; other characters show irregular geographic variation. The measured characters are statistically correlated. The variation of *T. m. harfordiana* is very narrow. The putative hybrid populations are more variable than either of the parents.

Triodopsis sanburni W. G. Binney
Plate VII: 15–18

Triodopsis sanburni W. G. Binney, 1886, 2nd Suppl., Bull. Mus. Comp. Zool. 13: 37, pl. 1, fig. 9; pl. 3, fig. 3. Kingston, Shoshone County, Idaho. Paratypes MCZ 53463 and 133029.

Triodopsis mullani subsp. *magnidentata* Pilsbry, 1940, Monogr. Acad. Nat. Sci. Philadelphia, No. 3: Land Mollusca of North America 1 (2): 862, fig. 499 f, f'. Mission Creek, 7 or 8 miles above Jaques Spur, Nez Perce County, Idaho. Type ANSP 171243.

Definition. Triodopsis sanburni combines the taxa formerly known as *T. sanburni* and *T. mullani magnidentata.*

Description. Shell width 10.1–11.3 mm; height 5.8–7.0 mm, height to width ratio 0.54–0.62; umbilicus half covered by reflected edge of aperture; number of whorls 5.5–5.8, whorl to width ratio 0.50–0.54; embryonic whorls 1.4–1.5, coarsely striated below suture; striae broken into granules towards their ends; embryonic shell smooth elsewhere; the following one and one-half whorls with fine transverse striae and papillae (in contrast to Pilsbry, 1940: 859, who claims that "no hairs and no regularly arranged points [papillae] such as appear in . . . *T. mullani*" are present); subsequent whorls with 2–3 striae per millimeter on their upper side, striae alternately weak and strong; underside of shell with weak striae only; some shells possibly with very fine spiral and transverse lines as in *T. mullani* and *T. devia,* but this cannot be seen clearly because shells are worn; aperture low square, with a moderate or very thick lip swelling and moderately large lip teeth; upper lip tooth marginal or somewhat receding, lower lip tooth marginal or a bit bulging out of aperture; parietal lamella large and straight, sometimes slightly concave.

Differential diagnosis. Triodopsis sanburni differs from *T. m. mullani* in its smaller dimensions, larger lip teeth and parietal lamella, and tighter coiling of the shell. Also, its umbilicus is always half covered, whereas that of *m. mullani* is often open.

Distribution and ecology. Triodopsis sanburni occupies a restricted area in northern Idaho (Fig. 24). It is completely overlapped by *T. m. mullani,* a closely related form. This is rather rare in *Triodopsis* and, generally speaking, in any animal group, since closely related forms are expected to occur allopatrically, in accordance with the theory of geographic speciation. The *T. n. vulgata-fraudulenta* and *a. albolabris-dentifera* pairs can be cited as the only other exceptions to this rule in *Triodopsis.*

The *measured material* comes from the following localities: *Idaho*: Shoshone and Kootenai counties (2 samples each, MCZ); Nez Perce County (ANSP). A total of 5 samples, 1–5 specimens each, 12 specimens altogether.

All specimens were found in valleys or near lakes, between 1600 and 3500 feet elevation.

Variation. Triodopsis sanburni has rather a narrow range of variation, probably because of its small populations and limited

TABLE XIV

MEASUREMENTS OF REPRESENTATIVE SAMPLES OF *TRIODOPSIS M. MULLANI*, *T. M. MAGNIDENTATA*, AND *T. SANBURNI*. THE ARROWS POINT TOWARD THE TAXON TO WHICH *MAGNIDENTATA* BEARS THE GREATER SIMILARITY. ON THIS BASIS, *M. MAGNIDENTATA* IS CONSIDERED SYNONYMOUS WITH *SANBURNI*.

				Mean of		
Name	Remark	Locality	No. of specimens	Width in mm	Height to width ratio	Whorl to width ratio
m. mullani	average	Spokane County, Washington	11	15.3	0.53	0.35
m. mullani	smallest, with highest whorl to width ratio	Kootenai County, Idaho	3	12.7	0.50	0.39
m. magnidentata		Nez Perce County, Idaho	1	11.0 ↓	0.51 ↑	0.48 ↓
sanburni		Kootenai County, Idaho	4	10.5	0.58	0.51
sanburni		Kootenai County, Idaho	5	10.8	0.56	0.52

area of distribution. A correlation between shell width, height, and whorl number can be observed, as is customary in *Triodopsis*. Geographically, all characters vary irregularly.

Systematics. The form described as *Triodopsis mullani magnidentata* is said to differ from *T. sanburni* "by the strongly depressed shape and the fewer, less closely coiled whorls" (Pilsbry, 1940: 862). My measurements (Table XIV) show, however, that *magnidentata* is nearly identical with *sanburni* in these supposedly diagnostic features. For this reason, I consider *magnidentata* synonymous with *sanburni*.

Evolutionary relationships. Judging from the fact that *T. sanburni* is found in a much smaller area than the closely related *m. mullani*, we may infer that it has evolved from the latter. The fact that it is completely overlapped by *m. mullani* could be taken as an indication that it evolved through sympatric speciation; because, if it had evolved through geographic speciation, one would expect it to be allopatric to *m. mullani*. It is easy to see, however, that in a mountainous area like that of *sanburni*, local populations can become isolated and thus may speciate even in the center of the range. Secondary overlap could easily occur afterwards. Thus this case can be satisfactorily explained in terms of geographic speciation.

It is also interesting to note that while *sanburni* has achieved reproductive isolation from *m. mullani*, another descendant of the latter, *m. harfordiana*, has failed to do so, despite the fact that morphologically it is at least as dissimilar from *m. mullani* as is *sanburni*. Thus it appears that in *m. harfordiana* the development of reproductive isolating mechanisms has lagged behind that of morphological isolation, whereas in *sanburni* the two processes were concomitant. Similar cases are cited elsewhere in this paper (p. 236).

Summary. Triodopsis sanburni is a monotypic species; it includes the former *T. mullani magnidentata* as a synonym. It has a small population, a restricted area of distribution, and a narrow range of variation. It probably evolved from the ancestral *mullani* stock, through geographic isolation.

Triodopsis devia (Gould)
Plate VII: 1–3

Helix devia Gould, 1846, Proc. Boston Soc. Nat. Hist. 2: 165. Puget Sound, Washington. Type not seen.

Helix baskervillei Pfeiffer, 1850, Proc. Zool. Soc. London for 1849, 17: 130. Vancouver Island. Type not seen.

Definition. The name *devia* is used here in the conventional sense, including *baskervillei.*

Description. Shell width 19.4–26.0 mm; height 12.0–17.4 mm, height to width ratio 0.60–0.67; umbilicus almost entirely covered by reflected edge of peristome; number of whorls about 5–6; embryonic whorls 1.4–1.5, coarsely striated below suture; striae broken up into granules towards their ends; subsequent one and a half whorls with papillae and extremely fine striae, perhaps with hairs on papillae; remaining whorls striated, one strong and two or three weak striae per millimeter; strong striae rapidly subsiding towards periphery of whorl; intervals between striae with extremely fine spiral and transverse wrinkles, about 30 spiral wrinkles per millimeter; deep spiral grooves appearing after breakage; aperture square, lip swelling thick, marginal; lower lip tooth broad and very low, located near columella; upper lip tooth absent; parietal lamella short, low, sometimes merely a callosity.

Differential diagnosis. Triodopsis devia is distinguished from the related species *m. mullani* and *sanburni* by its greater size and by the fact that its lower lip tooth is located nearer to the columella than that of *m. mullani* and *sanburni.*

Distribution and ecology. Triodopsis devia occurs in the coastal area from Vancouver Island to Oregon (Fig. 24). Its area is separated from that of the related species *mullani* by the Cascade Range. At the point, however, where the Columbia River breaks through the mountains, the two species are in contact. *Triodopsis devia* is restricted to low elevations, below 600 feet. Pilsbry mentions (1940: 858) that it was found in damp places.

The *measured material*, all MCZ, comes from the following localities. *Washington*: King (2 samples), Pierce, Thurston, and Clark counties. *Oregon*: Hood River County. A total of 6 samples, 1–2 specimens each, 8 specimens altogether.

Variation. No appreciable variation can be seen on the available, very limited material.

Evolutionary relationships. Triodopsis devia is probably derived from *m. mullani*, which seems to be the central stock of the *mullani* complex. It is less likely that *devia* would be the ancestral form, because its range is peripheral to that of *m. mullani.* Furthermore, *m. mullani* shows greater affinity than *devia* does to *sanburni* and *m. harfordiana*, the other members of the complex.

Summary. Triodopsis devia is a monotypic species, of limited distribution and variation. It prefers low elevations. It is probably a descendant of *m. mullani.*

Triodopsis germana (Gould)
Plate VII: 19–23

Helix germana Gould, *In*: Binney, 1851, the Terrestrial Airbreathing Mollusks of the United States 2: 156, pl. 40a, fig. 3. Gould gave "Oregon" as type locality. Pilsbry (1940: 974) restricted the type locality to Astoria, Clatsop County, Oregon. Type not seen.

Polygyra germana vancouverinsulae Pilsbry and Cooke, 1922, Nautilus 36: 38. Cameron Lake, under dead bark on the ground, in open pine forest, Vancouver Island, British Columbia. Type ANSP 44538.

Definition. Triodopsis germana combines two taxa formerly considered separate subspecies: *g. germana and g. vancouverinsulae.*

Description. Shell width 6.6–6.8 mm; height 4.1–5.7 mm, height to width ratio 0.58–0.70; number of whorls 4.9–5.5, whorl to width ratio 0.62–0.78; umbilicus closed or almost closed; embryonic whorls 1.4–1.5, with papillae below suture; papillae arranged in transverse rows; subsequent whorls with fine transverse striae and papillae, rows of papillae becoming oblique; each papilla bearing a long, thick hair; last whorl slightly angular at its periphery; aperture oval or slightly auriculate; lip swelling moderately thick except near junction of upper lip with shell, where obsolete; no lip teeth; parietal lamella long and straight, very low, higher only at its upper end.

Differential diagnosis. Triodopsis germana is different from all other species of *Triodopsis* by virtue of its small and hairy shell, almost closed umbilicus, long and low parietal lamella, and absence of lip teeth. It looks very much like a *Stenotrema*. Only its anatomy shows that it belongs in *Triodopsis*.

Distribution and ecology. Triodopsis germana is known from the coastal region and the lower valleys of Oregon, Washington, and British Columbia. It never occurs higher than 500 feet (Fig. 24). It has been reported from open pine forests on Vancouver Island.

Variation. The whorl to width ratio tends to decrease from the north to the south. This may be a true clinal variation, but one cannot eliminate the possibility that chance alone causes it, since only a few samples are known. The width and height to width ratio show slight and irregular geographic variation.

Systematics. Triodopsis g. vancouverinsulae was subspecifically separated from *g. germana* because it is "in the average smaller, distinctly perforate, with a shallower furrow behind the outer and basal margins of the lip, a less prominent crest preceding it. Sculpture as in *germana* [*g. germana*], but the hairs generally lost in the adult stage" (Pilsbry, 1940: 874). These distinctions are valid if only the type populations are considered. When more samples are studied, it becomes evident that they do not hold true. The size of the shell, the furrow behind the aperture, and the crest that precedes it may be nearly equal in the two alleged subspecies. According to the figures by Pilsbry (1940: figs. 505 C and D) the hairs are much scarcer in *g. vancouverinsulae* than in *g. germana*. But in this character, too, the two forms intergrade. Consequently, I propose to consider *g. vancouverinsulae* synonymous with *g. germana*.

The *evolutionary relationships* of *Triodopsis germana* are completely obscure. It is so different in shell characters from all other species of the genus that not even an approximate guess can be made about its evolutionary relationships with them. It is included in the subgenus because of its anatomy and distribution.

Summary. Triodopsis germana is a monotypic species. The former *T. g. vancouverinsulae* can no longer be recognized as a separate subspecies; instead, it must be considered synonymous with *germana*. The species occurs in the northern Pacific coastal region, always at low elevations. It probably shows clinal variation in whorl to width ratio, but in other characters it varies irregularly. Its evolutionary relationships with other species of the genus are obscure.

Summary of Systematic Treatment

In conclusion, let us compare the classification proposed in this paper with that current in the literature (Table XV). In contrast to the 19 monotypic and 12 polytypic species with 41 subspecies of the current system, the new classification recognizes only 13 monotypic and 9 polytypic species with 21 subspecies. Thus, the number of taxa is reduced from a total of 60 to 34, that of the species from 31 to 22, notwithstanding the fact that some old taxa have been split, and a new subspecies described.

The reduction of the number of taxa was not the main goal of the study. It is rather the by-product of the use of quantitative methods and the consistent application of the biological species concept of the group studied. These led to the synonymization of poorly distinguished taxa with recognized species or subspecies, and to the combination of intergrading taxa (primary or secondary) in one species. Thus arose a greatly simplified system.

For assigning taxonomic rank to closely related, allopatric populations, the "yardstick method" has been recommended (Mayr, Linsley, and Usinger, 1953: 103). In principle, the method is correct, but there seem to be so many exceptions to it in *Triodopsis* that its use was abandoned. For example, *Triodopsis f. fallax* looks at least as different from *T. f. alabamensis* as *T. tridentata* does from *T. c. complanata*, and yet the former two taxa hybridize, the latter two are reproductively isolated. Similarly, *T. j. juxtidens* and *j. stenomphala*, *T. c. copei* and *c. cragini*, *T. o. obstricta* and *o. denotata*, and *T. m. mullani* and *m. harfordiana* are morphologically as different from one another as *T. fraudulenta* or *T. pendula* is from *T. n. vulgata*, or *T. a. albolabris* from *T. dentifera*, or *T. m. mullani* from *T. sanburni*, yet the former pairs interbreed, the latter do not. Instead of using the degree of morphological similarity as a yardstick, therefore, each case was judged on whatever evidence was available.

EVOLUTIONARY PROBLEMS

The term "evolutionary" is used here in a broad sense, including aspects of evolutionary biology as diverse as speciation, isolating mechanisms, hybridization, and adaptiveness and irregularity of geographic variation.

SPECIATION

The theory of geographic speciation is so firmly established that one can take it for granted that it also applies to *Triodopsis*. Nevertheless, it seemed worthwhile to make a brief study of the speciation in *Triodopsis*, which belongs to a lower and less studied group than *Drosophila* or the birds.

The study consisted of preparing hypothetical models, one for geographical speciation, another for sympatric speciation, and comparing the observed situation with these models. If speciation took place through geographic isolation, we should find the most closely related forms, that is, the incipient or very recently developed species, occurring allopatrically. If speciation took place according to the model of sympatric speciation, we should find the most closely related forms occurring sympatrically. The distribution of the more distantly related forms is less illuminating, since during their longer existence their range of distribution may have changed profoundly. In addition, the evolutionary relationships are often obscure among these older forms. For these reasons, the distribution of the distantly related forms was not considered.

Accordingly, the most closely related taxa were combined into pairs, and the pairs were classified according to distribution (Table XVI and Fig. 25). In 8 of the 20 cases (40%), the members of the pair are spatially separated from one another, in 9 cases (54%) they are in contact or slightly overlap, and in 3 cases (6%) they extensively overlap.

These data illustrate that speciation in *Triodopsis* was predominantly geographic. The first group (40%) is clearly indicative of speciation through geographic isolation. The second group (54%) also indicates geographic speciation, since it is much easier to assume that the narrow overlap is secondary than it is to assume that both overlapping taxa originated in the overlap zone, through sympatric speciation, and are now moving away from one another. The third group (6%) could possibly be interpreted as indicative of sympatric speciation. But the *T. fraudulenta-T. n. vulgata* and *T. m. mullani-T. sanburni* pairs occur in mountainous areas where spatial isolation is easy to achieve, and thus it seems very likely that spatial isolation played a role in the formation of these taxa. Only in the case of the *T. a. albolabris-T. dentifera* pair is the role of spatial isolation not evident. This is not to say that *dentifera* evolved from or gave rise to *a. albolabris* through sympatric speciation. It merely points out that the distribution of these taxa does not conform to the pattern generally considered "normal." One possible reason for this is that the deceiving morphological similarity between the two taxa actually conceals a more distant evolutionary relationship.

Table XV

Comparison of the Currently Used Classification with That Proposed in This Paper. The Former is a Compilation from the Works of Pilsbry (1940), Hubricht (1950b, 1952a, 1952b, 1954, 1958), and Lutz (1950).

Current classification: Species	Current classification: Subspecies	Classification adopted in this paper: Subspecies	Classification adopted in this paper: Species
	Subgenus: *Triodopsis*	Subgenus: *Triodopsis*	
tridentata	*t. tridentata*		*tridentata*
	t. edentilabris		
	t. juxtidens	*j. juxtidens* *j. stenomphala*	*juxtidens*
	t. discoidea	*j. discoidea*	
	t. complanata	*c. complanata*	*complanata*
	t. tennesseensis		
platysayoides		*c. platysayoides*	
burchi			*burchi*
rugosa	*r. rugosa*		*rugosa*
	r. anteridon		
fulciden			*fulciden*
picea			*fraudulenta*
fraudulenta	*f. fraudulenta*		
	f. vulgata	*n. vulgata*	*neglecta*
neglecta		*n. neglecta*	
pendula			*pendula*
fallax	*f. fallax*	*f. fallax*	all except *claibornensis* belong to species *fallax*
	f. affinis	*f. obsoleta*	
palustris			
hopetonensis	*h. chincoteagensis*		
	h. obsoleta		
	h. claibornensis	combined with *n. vulgata*	
	h. hopetonensis	hybrid	
messana			
vannostrandi	*v. vannostrandi*		
	v. goniosoma		
	v. alabamensis	*f. alabamensis*	
vultuosa	*v. copei*	*c. copei*	*copei*
	v. henriettae	hybrid	
	v. vultuosa		
cragini		*c. cragini*	
soelneri			*soelneri*
	Subgenus: *Xolotrema*	Subgenus: *Xolotrema*	
denotata		*o. denotata*	*obstricta*
caroliniensis		hybrid	
obstricta	*o. obstricta*	*o. obstricta*	
	o. occidentalis	combined with *Mesodon sargentianus*	
fosteri	*f. fosteri*	*f. fosteri*	*fosteri*
	f. hubrichti	*f. hubrichti*	
	Subgenus: *Neohelix*	Subgenus: *Neohelix*	
albolabris	*a. albolabris*	*a. albolabris*	*albolabris*
	a. alleni	*a. alleni*	
	a. fuscolabris	intergrade	
	a. major	*a. major*	
dentifera			*dentifera*
multilineata			*multilineata*
divesta			*divesta*

TABLE XV
(*Continued*)

SPECIES	SUBSPECIES	SUBSPECIES	SPECIES
	Subgenus: *Cryptomastix*	Subgenus: *Cryptomastix*	
populi			
mullani	*m. mullani*		
	m. hemphilli		
	m. latilabris		all except
	m. tuckeri	*m. mullani*	*magnidentata*
	m. olneyae		belong to
	m. hendersoni		species *mullani*
	m. blandi		
	m. clappi	hybrid	
	m. magnidentata	combined with *sanburni*	
harfordiana		*m. harfordiana*	
sanburni			*sanburni*
devia			*devia*
germana	*g. germana*		*germana*
	g. vancouverinsulae		
TOTAL: 19 monotypic species	12 polytypic species with 41 subspecies	13 monotypic species	21 subspecies in 9 polytypic species

ISOLATING FACTORS AND ISOLATING MECHANISMS

Geographic (spatial) isolation, as shown above, is evident in many cases in *Triodopsis*. Thus, the Appalachian Mountains caused isolation and led to speciation in *c. complanata-burchi*, *rugosa-fulciden*, and *j. juxtidens-j. discoidea*. The Mississippi Valley has been the barrier between *n. vulgata-n. neglecta*, *fallax-copei*, and *a. albolabris-a. alleni*, and the Cascade Mountains the barrier between *m. mullani-devia*. A seemingly uninhabited gap separates *c. complanata* from *c. platysayoides* (8 cases altogether). Other, less obvious, examples of geographic isolation follow. *Triodopsis j. juxtidens* and *j. stenomphala* were probably isolated by the Delaware River Valley (Fig. 9), *o. denotata* and *o. obstricta* by the Ohio River Valley (Fig. 21), and *n. vulgata* and *pendula* probably by the Appalachian Mountains (Fig. 13; the distribution of *pendula* may be secondarily altered, however; see p. 180); 3 cases altogether.

It is assumed that the following pairs were spatially isolated in the past, but the nature of the one-time barrier is not clear. The pairs are: *tridentata-c. complanata*, *f. fallax-f. obsoleta*, *f. alabamensis-f. fallax*, *f. alabamensis-f. obsoleta*, *c. copei-c. cragini*, and *m. mullani-m. harfordiana* (Figs. 3, 17, 20, 24); 6 cases altogether.

The facts that river valleys serve as barriers to dispersal, in the case of *Triodopsis neglecta*, *fallax copei*, *albolabris*, and possibly of *juxtidens* and *obstricta*, whereas the rivers themselves serve as agents of dispersal, in the case of *juxtidens* (in another part of the range) and *fraudulenta* (pp. 166, 182), at first seem contradictory. But there is no real contradiction here. The vegetation that covers the wide, often flooded valleys of the lower sections of large rivers, such as the Mississippi, Ohio, and Delaware rivers, and the fauna that lives in this vegetation, are natural barriers to species of other habitats, notably upland and mountain forests. At the same time, the smaller rivers and creeks, such as the Kanawha and the Potomac rivers and their tributaries, are just as naturally carriers downstream of the mountain-inhabiting populations.

There is insufficient information on the occurrence of behavioral and physiological isolating mechanisms. At least one of them

Table XVI

Classification According to Distribution of Twenty Closely Related Taxon Pairs of *Triodopsis*.

A. Members of pair separated from one another by a barrier or gap	Barrier or gap	B. Members of pair in contact, or slightly overlapping		C. Members of pair extensively overlapping
c. complanata-c. platysayoides	gap of 150 miles	*j. juxtidens-j. stenomphala*	hybridize	*n. vulgata-fraudulenta*
c. complanata-burchi	Appalachians	*f. fallax* and *f. obsoleta-f. alabamensis*	"	*albolabris-dentifera*
rugosa-fulciden	Appalachians			*m. mullani-sanburni*
j. juxtidens-j. discoidea	Appalachians	*c. copei-c. cragini*	"	
n. vulgata-n. neglecta	Mississippi Valley	*o. obstricta-o. denotata*	"	
		m. mullani-m. harfordiana	"	
fallax-copei	Mississippi Valley			
a. albolabris-a. alleni	Mississippi Valley and gap	*f. fallax-f. obsoleta*	intergrade	
		a. albolabris-a. major	"	
m. mullani-devia	Cascade Range	*tridentata-c. complanata*		
		n. vulgata-pendula		
TOTAL: 8		9		3

must be responsible for the separation of *tridentata* from *c. complanata*, *j. juxtidens*, and *f. fallax*. Ecological isolating mechanisms are not involved (p. 153). Ecological isolation is, in any case, rare in *Triodopsis*. The only examples I know of are between *tridentata* and *c. platysayoides*, *tridentata* and *j. discoidea*, and the Virginia populations of *j. juxtidens* and *j. stenomphala*. Apparently ecological divergence develops much more slowly than morphological divergence in *Triodopsis*. The numerous cases of ecological exclusion which result when two sympatric species have similar or identical ecological preferences are witness to this statement. Ecological exclusion was found between *tridentata* and *c. complanata*, *tridentata-j. juxtidens*, *tridentata-j. discoidea*, *tridentata-f. fallax*, *j. juxtidens-f. fallax*, *j. juxtidens-f. obsoleta*, *o. denotata-fosteri*, and perhaps *a. alleni-multilineata* (8 or perhaps 9 cases altogether). As a rule, behavioral or physiological isolating mechanisms also develop more slowly than do morphological differences, as shown by the long list of the secondarily interbreeding populations (see below); in some cases, however, they may develop concomitantly with morphological differences, *e.g.*, between *tridentata* and *c. complantata*, *n. vulgata* and *fraudulenta*, *n. vulgata* and *pendula*, *dentifera* and *a. albolabris*, *sanburni* and *m. mullani*.

Hybridization

The term hybridization is defined by Mayr (1963: 110) as "the crossing of individuals belonging to two unlike natural populations that have secondarily come into contact." He distinguishes various kinds of hybridization. In *Triodopsis*, the kind he describes as allopatric hybridization is common. It is found in 5, or possibly 7, of the 22 species: in *juxtidens*, *fallax* (between *f. alabamensis* and both *f. fallax* and *f. obsoleta*), *copei*, *obstricta*, and *mullani*, and possibly in *neglecta*, *fallax* (between *f. fallax* and *f. obsoleta*), and *albolabris*.

Hybrids are conventionally recognized by comparing the coefficients of variation; populations with high coefficients of variation are considered hybrids, those with normal coefficients, parents. This method could not be employed in *Triodopsis*, since one of the putative parents always had higher coefficients than both the putative hybrids and the other parent (Fig. 26). To overcome this difficulty, the range of variation of the various populations was compared. The comparison was made by two slightly different methods. Either the

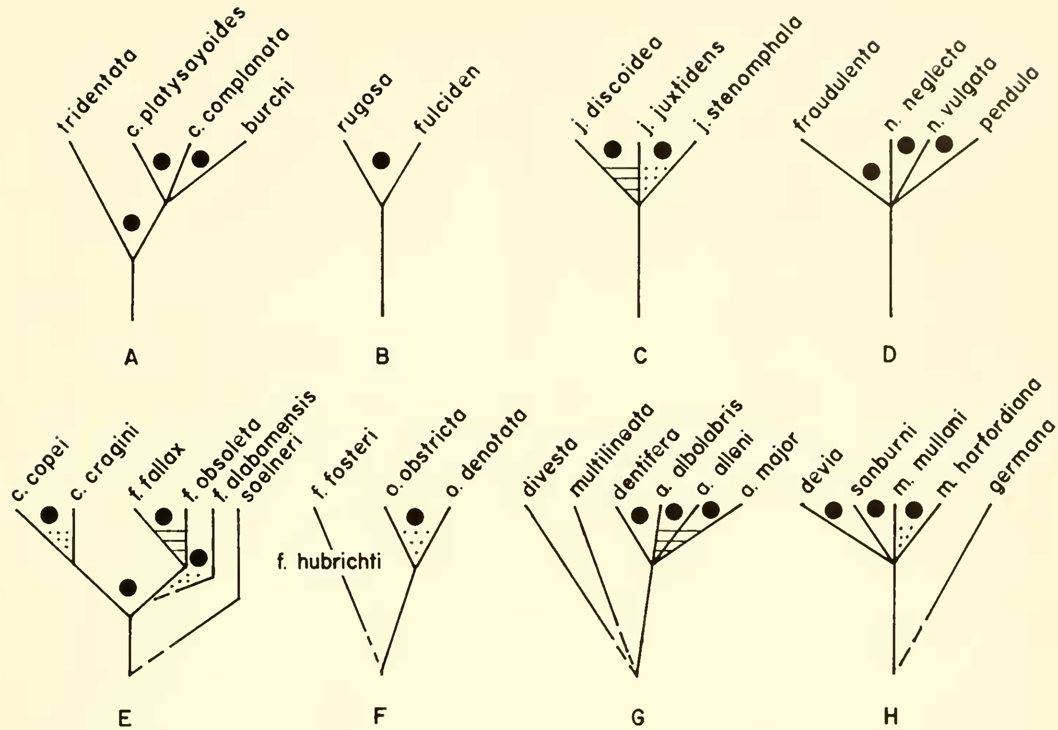

Figure 25. Assumed evolutionary relationships in *Triodopsis*. Solid dots mark the 20 closely related taxon pairs, utilized in making up Table XVI. Stippling indicates hybridization; horizontal lines, primary intergradation; dashed line, uncertain relationship.

range was plotted against population size (Fig. 27), or the natural samples were converted into samples of standard size, and the range of variation of these standardized samples was calculated and compared (Fig. 4; method adapted from Simpson, 1941). The advantage of the first method was that it avoided the use of the standard deviation, which is high in samples with a skewed distribution curve, and which, as may be recalled, is the situation in many hybrid populations of *Triodopsis*. The advantage of the second method is its clarity. Both methods were used for species in which samples with skewed distribution curves occurred. The second method was used alone in species with normal distribution curves.

The samples which showed considerably greater variability than the average were considered hybrids. These samples were always intermediate between two "parental" taxa, and they always occurred in the zone of contact between the two, or in a ring along the periphery of one of them (the latter also can be considered a contact zone, if we assume that one taxon is presently in the process of surrounding the other one). The morphological intermediacy and the described distribution pattern are consistent with the interpretation that the populations in question are of hybrid origin.

The range of variation in the hybrid populations is wider than normal, but it never spans the entire range of variation of the species, as is the case in some other hybrids. This may be because most of the characters utilized in the analysis of variation are polygenic; such characters often do

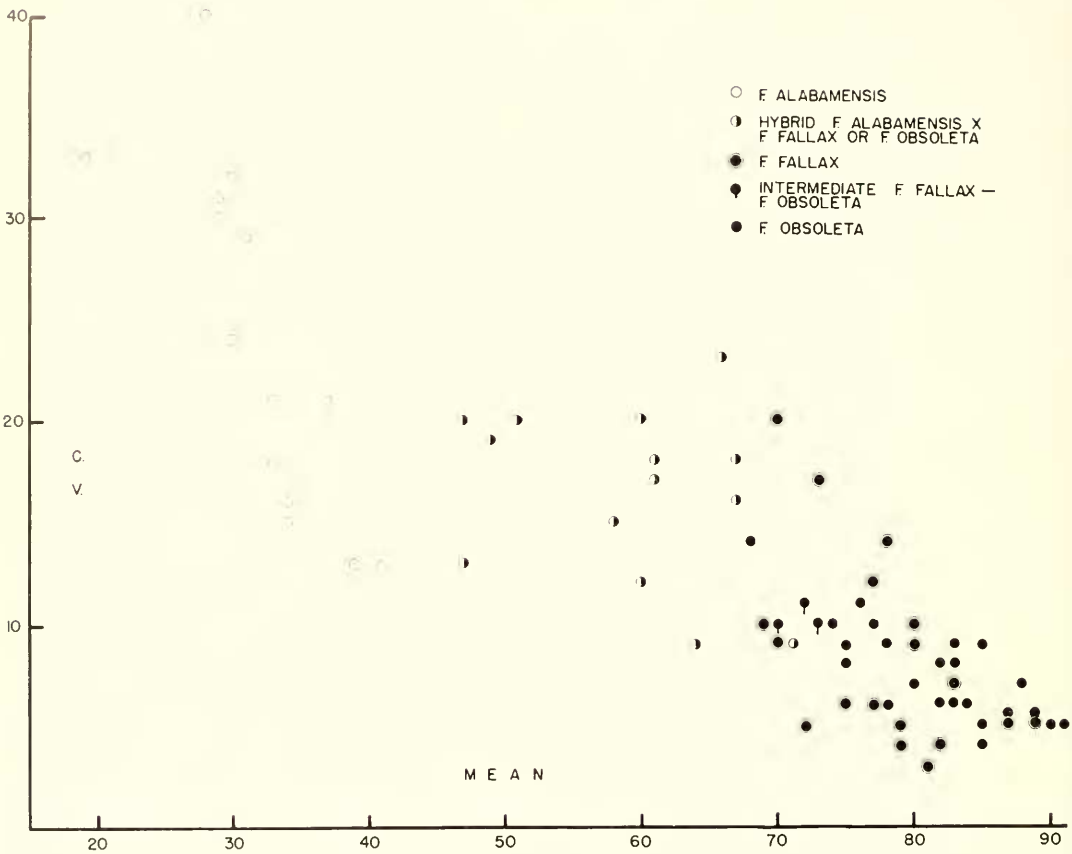

Figure 26. Scatter diagram of coefficient of variation (C.V.) versus mean in samples of *Triodopsis fallax*. Scale in character index units. The coefficient of variation tends to be inversely proportional to the mean. This is contrary to the expectation that hybrid samples will show higher coefficients than do the parental samples.

not show an appreciable increase in variation (Mayr, 1963: 131, 377).

It is possible that even supposedly "pure" populations of *T. f. alabamensis* have incorporated some genes from *f. fallax* or *f. obsoleta*. The populations of *f. alabamensis* are definitely more variable than those of *f. fallax* or *f. obsoleta* (Figs. 4, 27); a specimen of *f. alabamensis* from the interior of the range has a fulcrum, which normally occurs only in *f. fallax*. As the range of *f. alabamensis* is rather limited, it is easy to imagine that occasional specimens of *f. fallax* or *f. obsoleta* reach the heart of its range and interbreed there with the local *f. alabamensis* populations. This phenomenon approaches what is referred to as introgression by Anderson and Hubricht (1938). To use the term, however, would not be quite justified, because in our case only subspecies are involved, whereas introgression is usually applied to cases involving distinct species.

Adaptiveness of geographic variation

Those characters that appear in several, not directly related species, occupying the same area or habitat, can be considered adaptive to the particular area or habitat (Moore, 1949). In addition to such fundamental features as having a shell, coiling, etc., there are two shell characters in *Trio-*

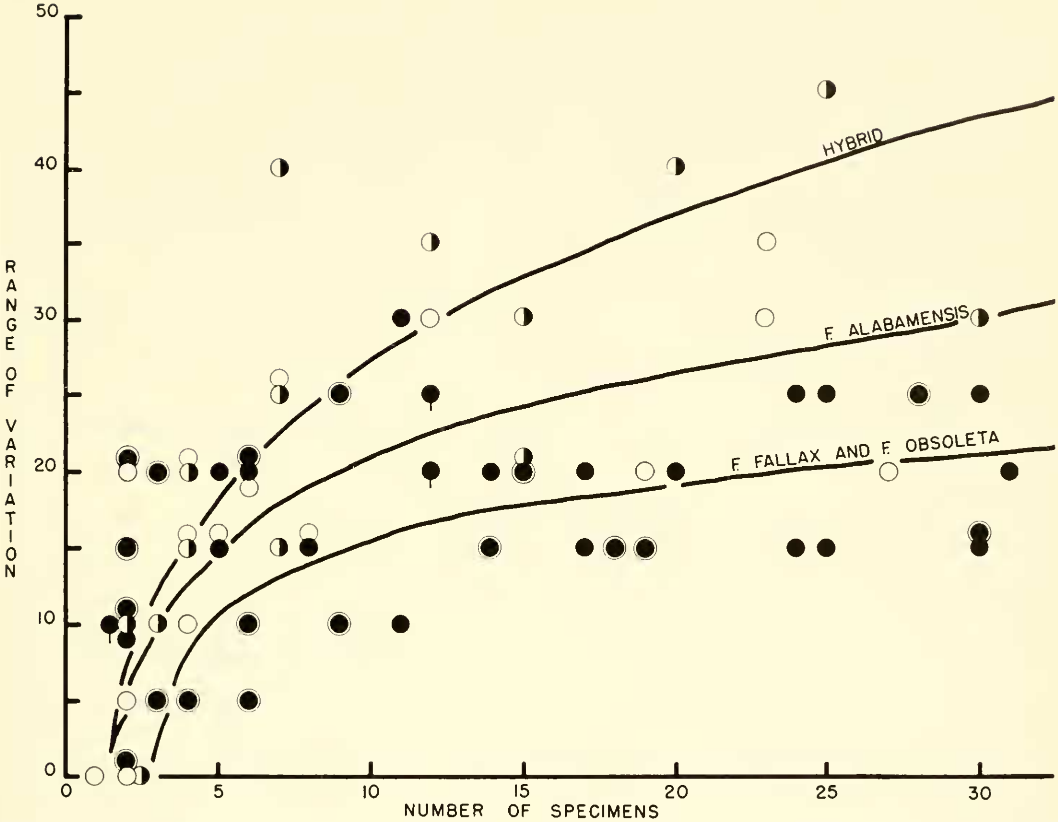

Figure 27. Scatter diagram of the range of variation in character index versus number of specimens in samples of *Triodopsis fallax*. Vertical scale in character index units. The hybrid samples have the widest range of variation, *f. alabamensis*, narrower, *f. obsoleta* and *f. fallax*, narrowest. Curves fitted by eye.

dopsis which satisfy the above requirements. One is the strong armature in mountainous areas, the other, the smooth sculpture in valleys.

Heavy armatures are observed in six species in *Triodopsis*. These are: *T. tridentata*, grades C and D, *rugosa, fraudulenta, f. fallax, c. copei* and *m. mullani*. Five of these forms occur in mountainous habitats; thus, *tridentata, rugosa* and *fraudulenta* in the Appalachians, *f. fallax* in the Blue Ridge Mountains, and *m. mullani* in the Cascade Range and the Rockies. The sixth form, *c. copei*, occurs however at low elevations, below 500 feet, in Texas (Fig. 20). The reason for its peculiar distribution is not known. Another anomaly is that *T. f. fallax* does not reach the peak region, but stops at about 1500 feet of elevation (Figs. 14, 15).

In spite of these two exceptions, it seems safe to conclude that the heavy armature is an adaptation to the mountainous habitat. This conclusion is supported by the case of *T. tridentata*, grades C and D, and *fraudulenta* and *f. fallax*. These three forms occur strictly allopatrically in the Appalachian and Blue Ridge Mountains (Fig. 14). They do so probably because they are all mountain-adapted, and thus they would compete for habitats with each other if they occurred sympatrically.

There is no explanation, however, of the significance of the heavy armature in mountainous conditions. The explanations proposed so far appear unlikely. For instance, Clench (personal communication) suggested that the large lip teeth and parietal lamella may be a protection against predators such as the beetles of the genus *Cychrus* and *Calosoma* (Ingram, 1950), because they obstruct the aperture and thereby make the entry of the predator difficult or impossible. However, there is no clear correlation between the occurrence of the predatory beetles and the heavy armature in the snails; the former occur in lowlands and mountains as well, the latter, only in the mountains (except *c. copei*). Thus Clench's suggestion cannot be the entire explanation, although it is not impossible that the heavy armature does give some protection against predators. Another obvious explanation could be that the strong armature depends upon the abundance of lime in the soil. But this idea also can be dismissed; heavy armature occurs on all kinds of rocks. Archer (1938), who also noticed the correlation between the armature and the elevation, did not produce any good explanation of the phenomenon. Knipper's conclusion (1939) that the armature is light in moist conditions and heavy in dry, apparently does not apply to *Triodopsis*, because the higher we go in the mountains the greater the precipitation. And even if it applied to *Triodopsis*, it could not be the explanation we are looking for, because it is simply another statement of an observation, not an explanation. It should be mentioned that Knipper studied European helicine and helicigonine snails, whereas Archer and I studied North American polygyrids (*Stenotrema* and *Triodopsis*, respectively); this may explain why Knipper found a correlation between armature and dryness, Archer and I, a correlation between armature and elevation.

The other apparently adaptive character is the smooth sculpture of the shell. It occurs in four or possibly five species in *Triodopsis*, that live in valleys, on the river banks, or near the river. Thus *T. c. complanata* has smooth populations in the valley of the Cumberland River, in Kentucky; *burchi* lives in the Dan River valley, in Virginia; *j. discoidea*, in the Ohio and Mississippi valleys, in Ohio and Missouri; and *c. platysayoides*, in the canyon of the Cheat River, in West Virginia. *Triodopsis m. mullani* also has smooth shelled populations, but the exact habitat of these populations is not known. These observations are comparable with Rensch's findings (1932). He wrote that land snails tend to have smooth, glossy, brown shells in cold climates, and white or strongly sculptured shells in hot ones. Why a smooth sculpture should be advantageous in cold climates or on the river banks remains, however, unknown.

Irregularity of Geographic Variation

According to Mayr (1963: 361), much of the geographic variation is clinal in continental species. Two of his main reasons are that (1) the selective factors (e.g., climate) change gradually, and thus the characters they act upon also tend to change gradually, and (2) gene flow tends to smooth out differences between adjacent populations.

In *Triodopsis*, however, very few clines occur. Eleven taxa are distributed over very restricted areas, and thus could not possibly develop clines. In the remaining 23 taxa, a total of 86 characters were measured and mapped; the characters included aperture, sculpture, keel, fulcrum, shell width, height to width ratio, umbilicus to width ratio, whorl to width ratio, and upper lip tooth to lower lip tooth ratio. Only eight characters (9.3%) vary clinally. Five clines are clear cut: the upper lip tooth to lower lip tooth ratio, in *tridentata*; the umbilicus to width ratio, in *rugosa*; size (width), in *j. discoidea*; aperture, from *f. obsoleta* to *f. fallax*; and whorl to width ratio, in *germana*. Three clines are less clear cut: the size and aperture, in *tridentata*, and the height to width ratio, in *a. alleni*. It is possible that the umbilicus to width ratio of *rugosa* should also be listed with the second group. As examples of clines, the variations of the umbilicus to width ratio in *T. rugosa*, and of the size (shell width) in *T. j. discoidea* are illustrated (Figs. 7, 12). Irregular geographic variation is exemplified by the variation of size and sculpture in the former and that of sculpture in the latter taxon (Figs. 8, 12).

The scarcity of clines in *Triodopsis* is evidently at variance with the expectation. The probable explanation is as follows. First, selective forces different from those affecting large animals act upon *Triodopsis* (or, speaking generally, upon small animals). Thus, for small animals the microclimatic factors are of prime importance, whereas for large ones, the macroclimatic factors are the most important. Second, the forces acting upon small animals vary more irregularly than those acting upon large ones. It is easy to see that the microclimate of a cool and humid northern slope contrasts sharply with that of a warm and dry southern slope, or that of an open plateau with that of a ravine; all of these places may, of course, share a very similar macroclimate. Since such habitats may occur repeatedly within one area, the resulting irregular variation is only to be expected.

It is most unlikely that absence of gene flow would cause the irregularity of geographic variation in *Triodopsis*, even though land snails are often (I think unjustifiably) cited as examples of sedentary species. Gene flow is observable in several species. Cases in which the hybrids form a ring around the range of subspecies A (Figs. 17, 20, 21) can best be explained by immigration (gene flow) from subspecies B into the scarcely inhabited, peripheral area of subspecies A, and subsequent interbreeding there between B and A. The gene flow cannot, of course, be restricted only to the peripheral areas, but must also occur inside the range. Additional evidence of the occurrence of gene flow is the fact that the hybrid zone between *j. juxtidens* and *j. stenomphala* does not quite coincide with the valley of the Delaware River, which presumably was once the isolating barrier between them, but lies east of that valley (Fig. 9). It seems that there is a "gene overflow" from the side of *j. juxtidens* toward *j. stenomphala* (the latter has a much smaller population), across the Delaware River valley. The "introgression" from *T. f. fallax* to *f. alabamensis* also supplies evidence of gene flow, as discussed above. Thus irregular geographic variation apparently occurs in spite of gene flow, not because of a lack of it.

SUMMARY

(1) With the use of quantitative methods and the application of the biological species concept, the systematics of the genus *Triodopsis* has been revised. One species has been divided into three separate species, and a new subspecies has been described. Nevertheless, because of repeated synonymizations the number of taxa has been reduced from 60 to 34, that of the species from 31 to 22. In detail, the number of monotypic species has been reduced from 19 to 13, polytypic species from 12 to 9, and subspecies from 41 to 21.

(2) There is overwhelming evidence that speciation in *Triodopsis* is predominantly geographic. Of 20 analyzed cases, this is virtually certain in 8, very likely in 9, probable in 2, undecided in 1. Geographic isolating barriers are common. Thus, the Appalachian Mountains served as such in 4 of the 20 analyzed cases, the Cascade Mountains in 1, the valley of the Mississippi River in 3, the Ohio River in 1, the Delaware River in 1, a gap between the two speciating populations in 1; in only 6 cases can no obvious geographic barrier be discerned (3 cases overlap).

Reproductive or behavioral isolation, but particularly ecological isolation, may develop much more slowly than do morphological differences, and one kind of isolating mechanism may precede the other. For this reason, the "yardstick method" of judg-

ing the degree of biological distinctness solely on the basis of morphological distinctness has been abandoned.

(3) Allopatric hybridization is common in *Triodopsis.* It occurs in 5 or possibly 7 of the 22 species. Some authors have considered as taxonomically distinct some of the hybridizing populations or the hybrids. However, these taxa have not reached either reproductive or ecological isolation; this opinion, therefore, is apparently incorrect.

The hybrid populations are recognized by their greater variation, morphological intermediacy, and occurrence in the zone of contact between the parental populations. The range of variation was used for ascertaining the extent of variation; coefficients of variation could not be used for such purposes.

(4) A strong development of the aperture appears to be an adaptation to mountainous habitats, a smooth shell sculpture an adaptation to valley habitats. Strong armature is found in 6 of the 22 species, smooth sculpture in 4. The significance of these adaptations is unknown.

(5) The geographic variation is predominantly irregular. Only 8 clines have been found among the 86 cases analyzed. This is unexpectedly few in continental species. It is theorized that the irregularity of the geographic variation is due to irregularly changing factors such as the microclimate. The notion that lack of gene flow is responsible is rejected; gene flow is evidenced by the ring-shaped distribution of hybrids around some subspecies, "gene overflow" from *T. j. juxtidens* to *j. stenomphala* across the Delaware River valley, and "introgression" from *T. f. fallax* and *f. obsoleta* into *f. alabamensis.*

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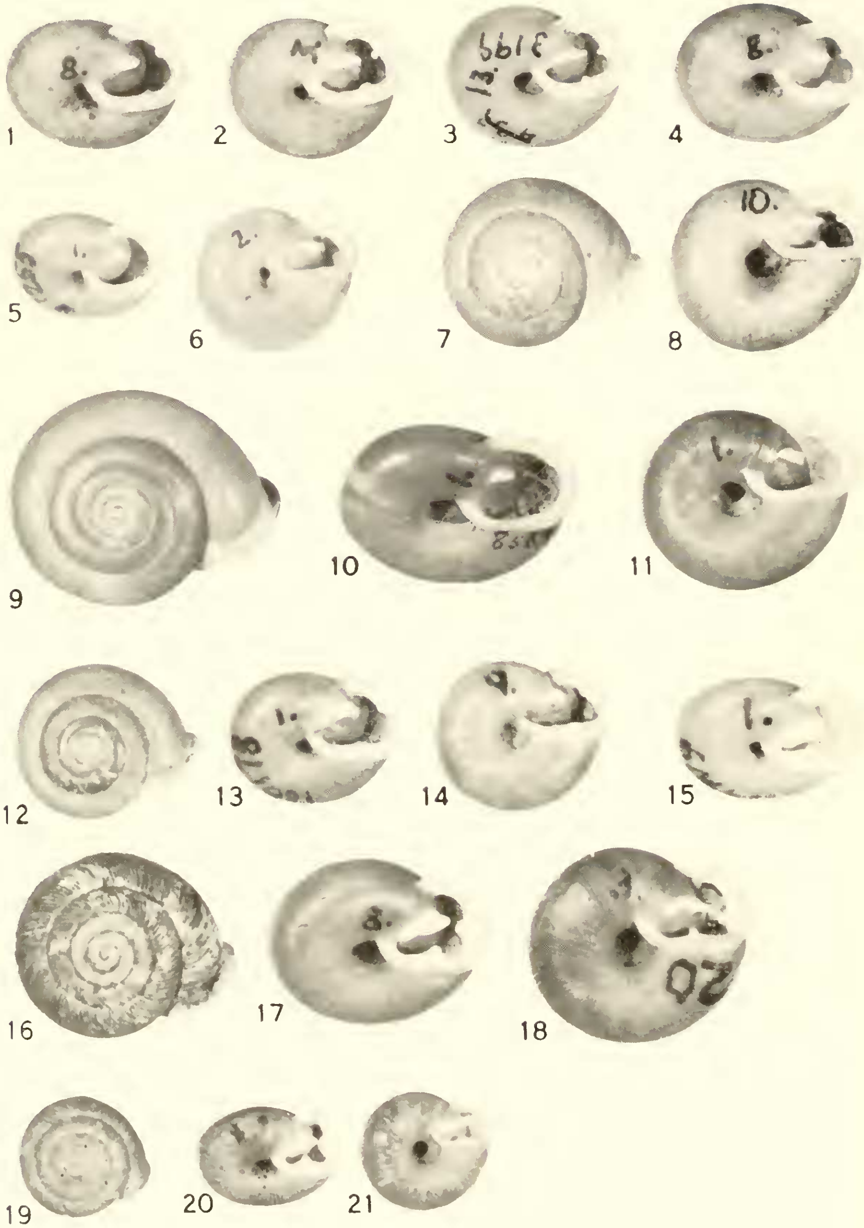

Plate I. The *Triodopsis tridentata* and *rugosa* complexes. 1–8, *Triodopsis tridentata*: 1 and 7, aperture grade A, Williston, Vermont; 2, aperture grade B, Bethel, Pennsylvania; 3, aperture grade C, Moores Hill, Indiana; 4 and 8, aperture grade D, Murphy, North Carolina; 5–6, *edentilabris*, considered synonymous with *tridentata*, aperture grade A, types, "Cumberland Mountains." 9–11, *Triodopsis c. complanata*: 9–10, Jamestown, Kentucky; 11, Boone, Tennessee. 12–14, *Triodopsis burchi*: 12 and 14, paratypes; 13, holotype, Danville, Virginia. 15–18, *Triodopsis rugosa*: 15, paratype, Blair, West Virginia; 16, Big Stone Gap, Virginia; 17–18, *anteridon*, considered synonymous with *rugosa*, paratypes, Valley Forge, Tennessee. 19–21, *Triodopsis fulciden*, Conover, North Carolina. Figures 1–8 are magnified × 1.6; figures 9–11, × 1.5; figures 12–21, × 2.2.

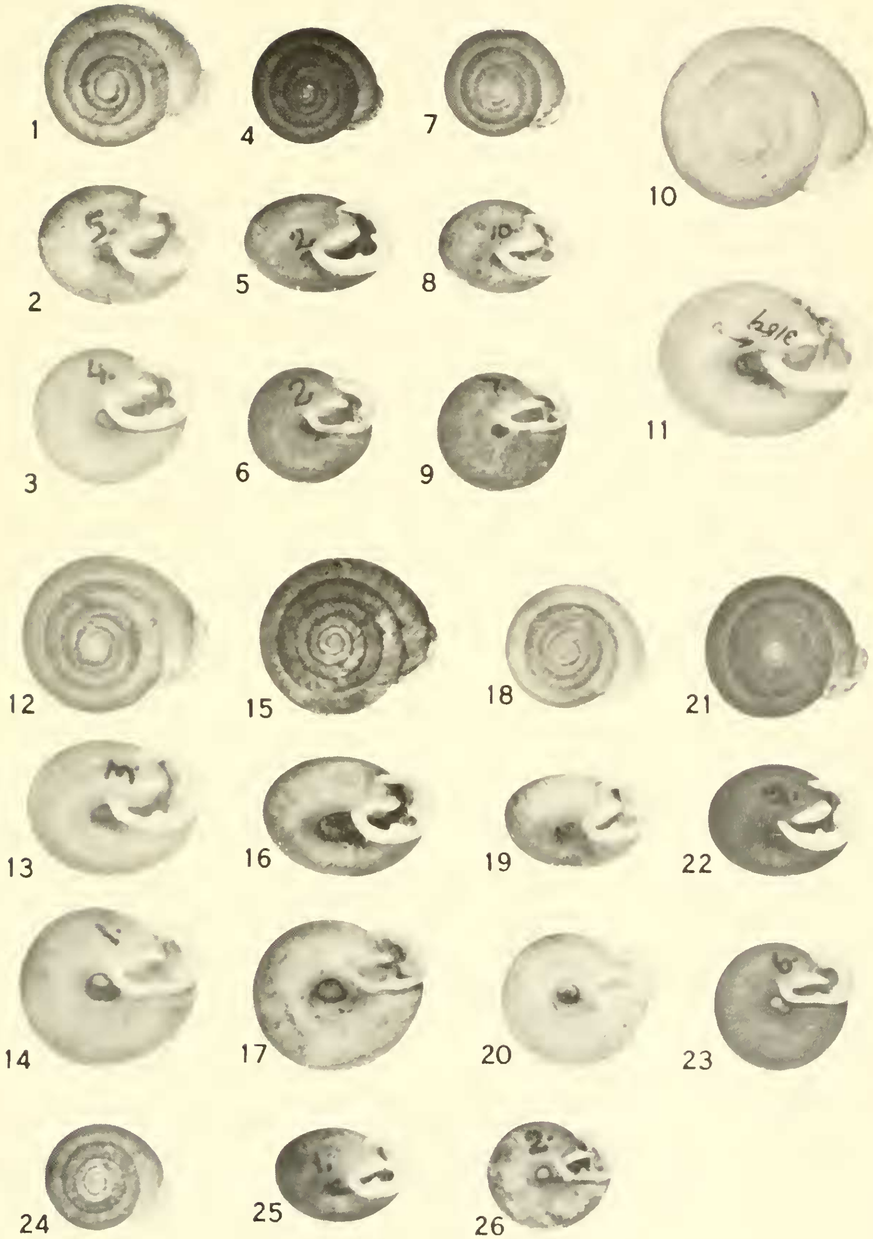

Plate 11. The *Triodopsis juxtidens* and *fraudulenta* complexes. 1–11, *Triodopsis juxtidens*: 1–2, *j. juxtidens*, Flatbrookville, New Jersey; 3, *j. juxtidens*, Richmond, Virginia; 4 and 6, hybrid *j. juxtidens* × *j. stenomphala*, Bedford, Virginia; 5, hybrid, Newark, New Jersey; 7, *j. stenomphala*, Dry Fork, Virginia; 8–9, Jenkintown, Pennsylvania; 10–11, *j. discoidea*, Cincinnati, Ohio. 12–20, *Triodopsis neglecta*: 12–14, *n. vulgata*, Ann Arbor, Michigan; 15–17, *n. vulgata* approaching *n. neglecta*, Huntsville, Alabama; 18–20, *n. neglecta*, Eureka Springs, Arkansas. 21–23, *Triodopsis fraudulenta*, Lewisburg, West Virginia. 24–26, *Triodopsis pendula*: 25, holotype; 24 and 26, paratypes, Hanging Rock State Park, North Carolina. Figures 1–9 and 12–26 magnified × 1.5; 10–11, × 1.9.

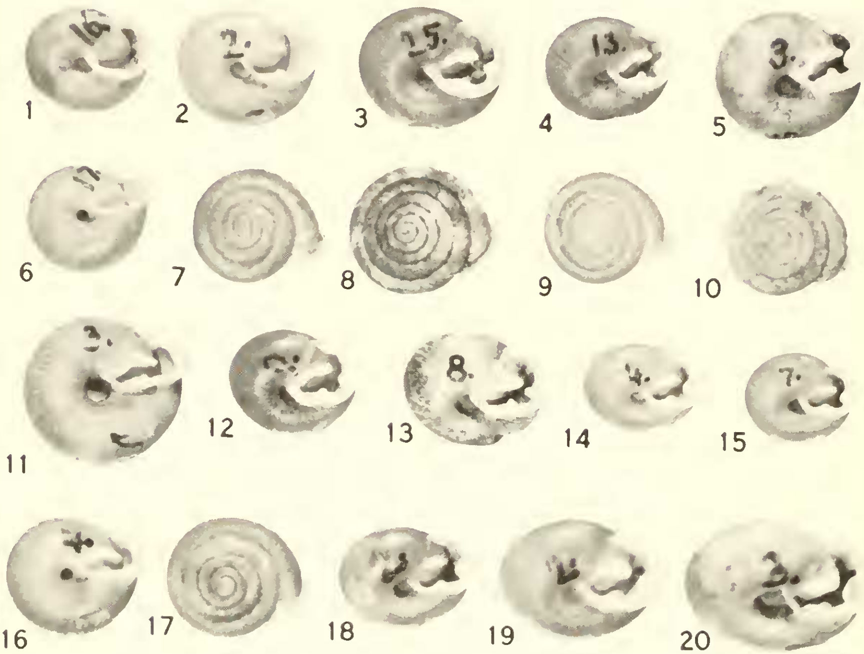

Plate III. The *Triodopsis fallax* complex. 1–15, *Triodopsis fallax*: 1, 6, and 7, *f. obsoleta*, aperture grade A, Trenton, North Carolina; 2, *f. obsoleta*, paratype, aperture grade A, Newbern, North Carolina; 3, *f. obsoleta*, aperture grade B, Rich Square, North Carolina; 4, *f. fallax*, aperture grade C, Marion, South Carolina; 5, *f. fallax*, aperture grade D, Seagrove, North Carolina; 10, *f. fallax*, aperture grade D, Chestertown, Maryland; 11, *f. fallax*, aperture grade D, Draper, North Carolina; 8 and 13, hybrid of *f. alabamensis* with *f. fallax* or *f. obsoleta*, or intermediate between the latter two subspecies, Aiken, South Carolina; 12, hybrid, Hartwell, Georgia; 9, 14, and 15, *f. alabamensis*, Langdale, Alabama. 16–20, *Triodopsis copei*: 16, *c. cragini*, aperture grade B, Arkadelphia, Arkansas; 17–18, *c. cragini*, aperture grade B, Chetopa Creek, Kansas; 19, hybrid *c. cragini* × *c. copei*, aperture grade C, Macdona, Texas; 20, *c. copei*, aperture grade D, Neches, Texas. Figures 1–15 are magnified × 1.5, 16–20 × 2.

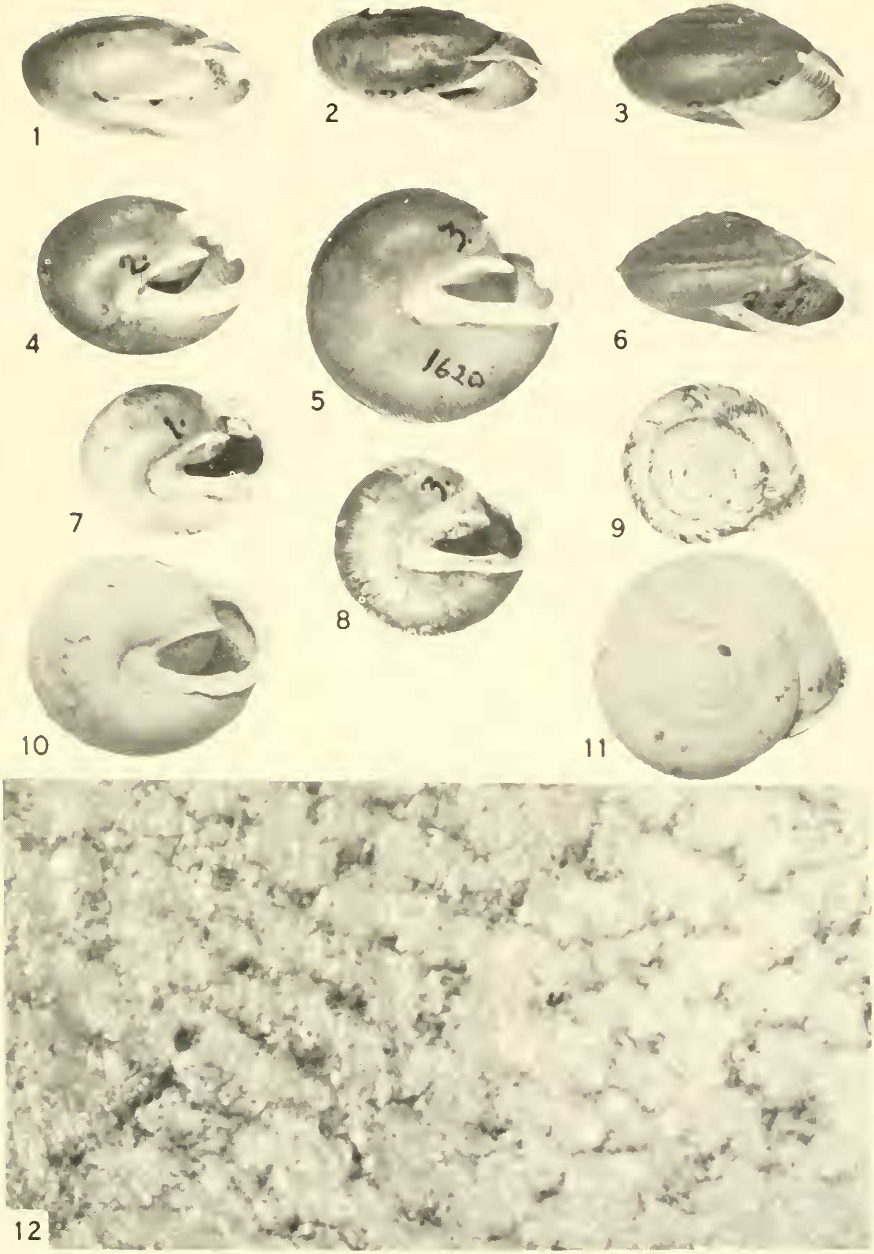

Plate IV. The *Triodopsis obstricta* complex. 1–6 and 12, *Triodopsis obstricta*: 1 and 4, o. *denotata*, angularity # 1, North Adams, Massachusetts; 2, hybrid o. *obstricta* × o. *denotata*, angularity # 2, Mt. Carmel, Illinois; 3, hybrid, angularity # 3, Frierson Mills, Louisiana; 5–6, o. *obstricta*, angularity # 4, Nashville, Tennessee; 12, sculpture of o. *denotata*, a portion of the last whorl shown, Annandale, New York. 7–11, *Triodopsis fosteri*: 7–9, f. *fosteri*, paratypes, Elizabethtown, Illinois; 10–11, f. *hubrichti*, paratypes, Valmeyer, Illinois. Figures 1–6 are magnified × 1.5; 7–9, × 1.6; 10–11, × 1.4; 12, × 40.

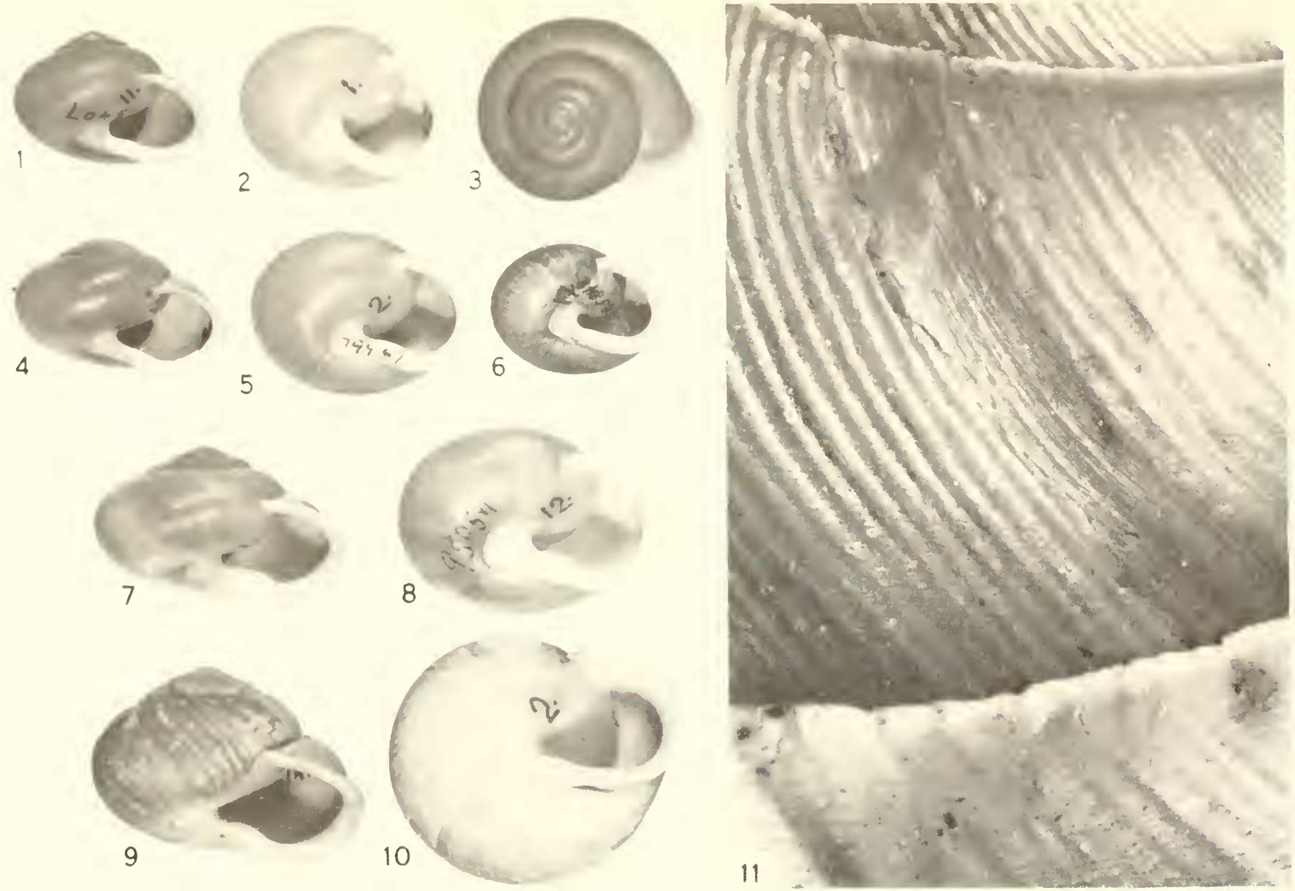

Plate V. *Triodopsis albolabris.* 1 and 3, *T. a. albolabris*, Orono, Maine; 2, *dentata*, Circleville, Ohio; 6, *maritima*, Biological Station, Michigan; the latter two forms are considered synonymous with *a. albolabris*; 11, sculpture of *a. albolabris*, portions of the last three whorls shown, with a breakage in the penultimate whorl (notice how much coarser the spiral lines become after the breakage); 4, *a. alleni*, Hamilton, Illinois; 5, *a. alleni*, paratype, Eureka Springs, Arkansas; 7, *fuscolabris*, considered intermediate between *a. alleni* and *a. major*, Woodville, Alabama; 8, *fuscolabris*, Huntsville, Alabama; 9, *a. major*, Murphy, North Carolina; 10, *a. major*, Elamville, Alabama. Figure 11 magnified × 15; all other figures, × 1.

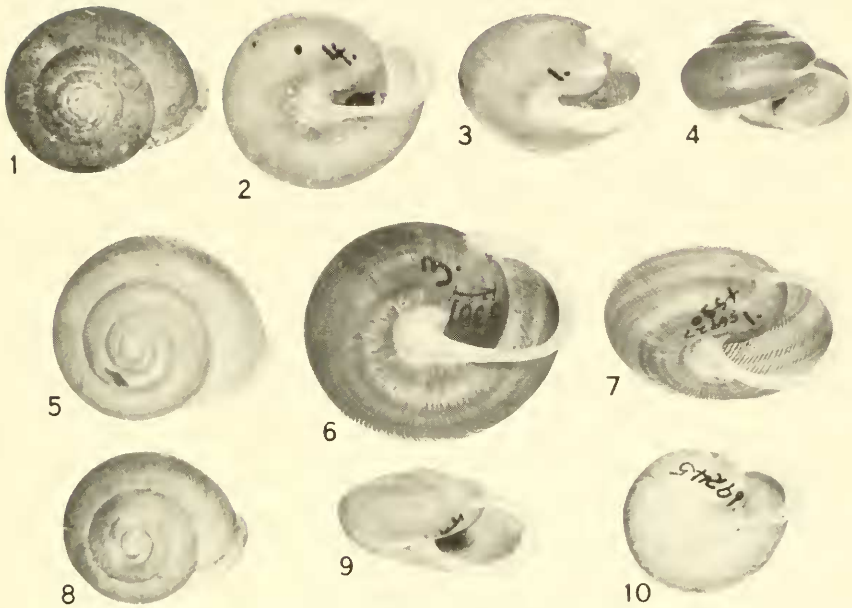

Plate VI. *Triodopsis dentifera, multilineata,* and *divesta.* 1–3, *Triodopsis dentifera*: 1, Rangeley, Maine; 2, Corrigain [or Cardigan?] Mountain, New Hampshire; 3, Vermont, labelled as "? cotype." 4–7, *Triodopsis multilineata*: 4, *algonquinensis*, cotype, considered synonymous with *multilineata*, Algonquin, Illinois; 5, Cincinnati, Ohio; 6, Mt. Carmel, Illinois; 7, Bluffton, Indiana. 8–10, *Triadopsis divesta*: 8, Hot Springs, Arkansas; 9, "Oklahoma"; 10, Cherokee County, Oklahoma. All figures magnified × 1.35.

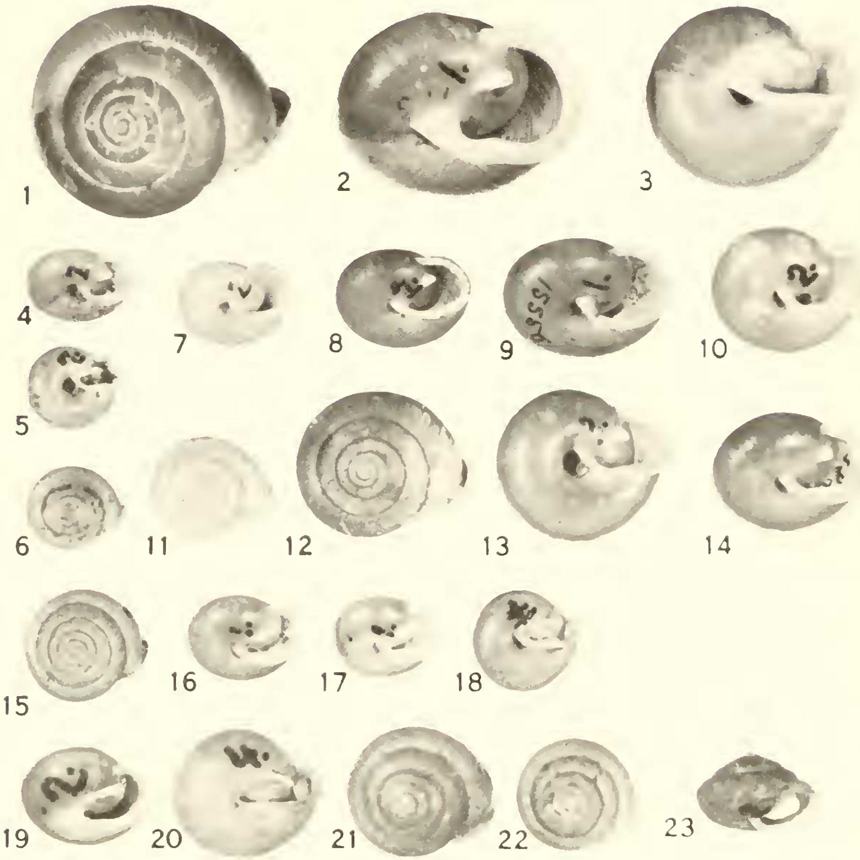

Plate VII. The *Triodopsis mullani* complex. 1–3, *Triodopsis devia*, Olympia, Washington. 4–14, *Triodopsis mullani*: 4–6, *m. harfordiana*, Salmon River, Idaho, 4 and 6 cotypes; 7 and 11, hybrid *m. harfordiana* × *m. mullani*, Salmon River, Idaho; 8, *blandi*, Post Falls, Idaho; 9, *hendersoni*, Weiser, Idaho; 10 and 13, *olneyae*, Selway Falls, Idaho; 12, *olneyae*, Libby, Montana; 14, *olneyae*, "Idaho"; the latter three forms are considered synonymous with *m. mullani*. 15–18, *Triodopsis sanburni*: 15 and 18, Kingston, Idaho; 16, Coeur d'Alene Mountains, Idaho; 17, Old Mission, Idaho. 19–23, *Triodopsis germana*: 19, Knapton, Washington; 20–21, Astoria, Oregon; 22–23, *vancouverinsulae*, considered synonymous with *germana*, Vancouver, British Columbia. Figures 1–18 magnified × 1.45; 19–23, × 2.30.

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